BREEDING BEEF CATTLE

IN A

RANGE ENVIRONMENT

papers presented at the

Fort Keogh Research Symposium

Miles City, Montana

September, 1984

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Edited by

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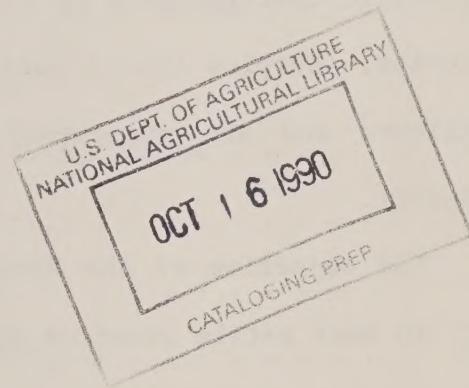
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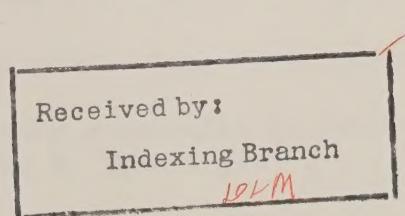
SYNOPSIS

The 1984 Fort Keogh Research Symposium was held on September 11 and 12, 1984, in Miles City, Montana. The Symposium was held in honor of the Line 1 Hereford project. The Agricultural Research Service of the USDA started several experiments on inbred beef cattle in the late 1920's and early 1930's. One of those experiments, the Line 1 Hereford project, is still active and 1984 marks its 50th anniversary. The project has provided major scientific contributions to both basic and applied knowledge of beef cattle genetics. Surplus Line 1 cattle have been sold to seedstock and commercial cattlemen and are recognized as an important asset to the beef cattle industry.

The objective of the Symposium was to (1) establish the "state of the art" in beef cattle genetics with special emphasis on the range environment; (2) provide interdisciplinary discussions of related animal and range science research as they affect and, in turn, are affected by past, present, future and potential variations in genotypes of range beef cattle; and (3) provide a setting for interactions among scientists and administrators from both the animal and range sciences.

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THE EVOLUTION OF RANGE CATTLE

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If we are going to select the "best" cattle for our rangelands, we must understand as much as possible about the biology of the animals and of the range plus the economics of the production systems. I hope to introduce the examination of the biology of the cattle in a manner that will complement the presentations of the range scientists and systems analysts who will follow me today.

An understanding of the evolutionary background to our cattle is a logical start to understanding how, why and where we want to change (select) them.

We can divide our discussion into five areas--each of which will address one question: (1) Where do we want to go?, (2) How do we get there?, (3) Where are we now? (4) How did we get here?, and (5) Where did we start?. Each question will be easier to answer if we can first answer the questions before it. I will start with question 5, then move to 4 and then 3 and comment briefly on questions 2 and 1. The overall objective of this symposium is to address questions 1 and 2 and I hope to lay some groundwork that will aid in achieving that objective.

(5) Where did we start?

Cattle as we know them probably originated in India and then spread over most of Asia, Europe and across Northern Africa (Herre, 1958). These cattle, Bos primigenius, are generally considered the progenitors of all domestic cattle, including the zebus (French et al., 1966). Darwin (1897) noted that cattle probably did not originate in areas with winter snow cover because cattle do not have the instinct to scrape away snow to get at forage as do horses or bison. Bos primigenius, also called urus or aurochs, were brown, black or red in cave paintings and skeletal remains have been examined to provide estimates of wither heights of 175 to 200 cm in bulls and 150 to 170 cm in cows.

Cattle were first domesticated in India, the Near East and Egypt between 6000 and 4000 B.C. (French et al., 1966) and in Switzerland during the Neolithic period (Darwin, 1897). Wild cattle were still present in central Europe during Caesar's time, and the last known uru cow died in Poland in 1627.

A second species, Bos longifrons, was present in Britain before 900 A.D. and was known to have been a food supply for the Roman legions. Because Bos longifrons was described as considerably smaller and finer boned than Bos primigenius and had different-shaped horns, it was once thought to have a separate origin. Most sources now consider Bos longifrons to be a descendant of Bos primigenius and evidence for selection effects on cattle at very early stages of domestication.

(4) How did we get here?

Darwin (1897) divided selection into three kinds. Methodical selection is a systematic attempt by man to modify animals to meet some predetermined standard or standards. Unconscious selection is selection by man without a definite goal in mind. A man will keep animals he likes and sell or destroy those which he dislikes even if the reason for liking or disliking is not clear. I think of methodical selection as producing a breed effect and unconscious selection as producing a breeder effect. The third type of selection is natural selection--individuals best suited to their environment generally survive and pass on their respective genes.

Methodical selection has been practiced on many traits in cattle. Cattle that were originally domesticated may have been selected for smaller overall size to make them more manageable. Draft animals have been selected for more muscling in the hindquarters. People that used milk kept the higher-milking cows. Different-colored hides had tribal or regional significance so selection for particular colors or color patterns has been wide-spread. Size and shape of horns, heads and legs have been altered by methodical selection. Darwin (1897) noted that "no point or character is too trifling to be methodically attended to and selected by breeders". We must remember, however, when we laugh at a program of selection for "fancy points" that these fancy points may have been important at some time and place.

Results of unconscious selection are often difficult to show directly. Temperament, size, bone structure, color pattern and even voice variations have probably all been selected for or against as herdsmen have preserved the animals that pleased them and sold, destroyed or neglected those that displeased them. Many showring characteristics are subject to unconscious selection. Animals win shows because they are "good" and they are "good" because they win shows and selections are made on this basis.

Natural selection is often referred to as survival of the fittest. This phrasing is misleading because it does not directly include the reproductive aspects of natural selection. As Spencer (1897) noted, "there is a constant struggle between self-preservation and race preservation". Selection acts at many times and the case of a cow simply failing to conceive can have essentially the same effect on a population gene pool as the more dramatic case of a young bull being killed in his first competition for females or an animal succumbing to disease, injury, predators or starvation. A cow raising twins contributes twice as much to the gene pool as a cow raising a single calf, but her contribution can go to zero if the twins do not reach breeding age. Natural selection has decreased in importance as herdsmen have been able to more effectively control or compensate for the vicissitudes of the environment in which cattle are raised, but natural selection is still an important factor that should not be ignored.

The three kinds of selection have acted separately and in combination to change cattle in many ways since they were domesticated. These changes have been in many directions and back and forth so that cattle today are a heterogeneous population with races and breeds sharing many common genes.

The population as a whole probably still contains most of the genes of the wild aurochs but arranged in different ways.

(3) Where are we now?

Because of the different forces of selection over the years, we are anywhere we want to be. Cattle have maintained high levels of heterozygosity and general genetic variation because of selection pressures which have been methodical, unconscious, natural or any combination.

Diversifying (or disruptive [Dobzhansky, 1970]) selection is a product of genotype-environment interaction. Different allelic complexes will be favored in different forms of organisms at different stages of growth and reproduction within different environments in various times and places. A genotype that is an advantage to a bull may be a disadvantage to a cow and vice versa. During times of high levels of nutrition, the allelic complexes that increase fertility are favored because of the high fecundity they bestow on their possessors. During a nutritional stress period, however, the high demands of reproduction can weaken and kill high-producing cattle and their progeny leaving the less fertile individuals with their low fertility allelic complexes as survivors. Even during prolonged periods of high potential levels of nutrition, overpopulation can deplete feed resources and create nutritional stresses. Any polymorphic population which is able to change its net fecundity along with environmental fluctuations has an overall superiority over other populations (Giesel, 1974). The phenomenon of a population lowering reproductive rates in the face of restricted food supply is common enough to have a name--Cole's result (Cole, 1954).

Stabilizing selection forms an outer framework to the diversifying selection. As Haldane (1954) observed, stabilizing selection on a quantitative character acts to "weed out" the extremes. A stabilizing framework in fertility in cattle acts through those which don't reproduce at all at one end and cows that produce so many offspring that they are unable to care for them (or themselves) at the other end. In alleles affecting growth, one end is represented by individuals that fail to survive due to too little growth which makes them too small for reproduction or too weak for nutritional or reproductive competition, and the other end by individuals that grow so fast that nutritional requirements will exceed availability. Only since the development of winter feed supplements in the 18th century and our more recent development of mechanical means of gathering and storing winter feeds have cattle been spared the wide seasonal fluctuations in nutrient availability.

Thus, although cattle have been selected for centuries, they are by no means fixed genetically. Rather, they are in a balance. Wright (1978) preferred the term "poise" rather than "balance", which strikes me as an apt term. The cattle are "poised" and ready to go any direction we want to take them.

(2) How do we get there?

Perhaps we should define where we want to go before we decide the best way to get there. I have, however, seen few, if any, selection programs with a

definite goal. Most are open-ended. Selection pressure is placed on a characteristic or index of characteristics with a stated objective of "improving" that measure. "Maximum" rather than "optimum" is too often the objective.

Research data is available for use in designing selection programs. We have heritabilities of most growth measures and some reproductive measures. Most breeds and biological types of cattle have been characterized for performance measures. Selection response can be predicted in most cases. Different systems of crossbreeding have been tested and results published. As more research results come available, we should be able to predict growth and reproduction responses of any selection scheme.

We must, however, consider the whole animal and not just one measure when we select. When we change one aspect of an animal, how do we change that animal's overall fitness? We have estimates of genetic correlations among most growth traits so we can predict correlated responses to selection for the growth traits. We don't however, have estimates for genetic relationships among reproduction and fitness traits. Sadleir (1969) pointed out that "any factor affecting growth will also affect the onset of puberty".

Newton's third Law of Motion states that "for every action, there is an equal and opposite reaction". I think the same principle holds true in genetics. For every change we make through selection, there will be an opposing compensatory change somewhere in the animal. A significant part of our job as animal breeders is to identify and evaluate that reaction.

An example of an area where we must be careful in our selection programs is in the area of carcass fat. Swine breeders, who selected strictly for lean tissue growth, ended up with pigs that had depraved appetites and thermoregulatory and reproduction problems. Before we attempt to alter the fat deposition patterns of cattle, we should know why they are as fat as they are and why the deposits are in each particular area. Are steroids stored in some fat tissues but not in others? How dynamic is fat? What is the purpose of marbled fat? We may find that a certain level of fat is absolutely essential to all body processes and should be changed only slightly. Conversely, we may find that fat is not essential above a certain level and that most of the fat on cattle as we know them serves little purpose. After all, as Mason (1973) noted, until the development of fossil fuels, the most important part of a cow's carcass was the tallow. In the parts of the world where human dietary energy is not as abundant as it is in North America, the fat in cattle may be more important to the people than it is to the cattle. Whenever we select cattle, we must consider the biology of the whole animal and remember Dobzhansky's warning that "nothing in biology makes sense unless considered in the light of evolution".

(1) Where do we want to go?

There is no one "best" cow. Different cattle are suited best to different environments. Because we have difficulty in adequately describing both the cattle and the environment, we have difficulty in matching them at an optimum level. Plus, we have the complication on the Great Plains that the

cattle that are best suited to our environment are not necessarily the cattle that the feeders and packers want.

With all of these complications, the value of a systems approach to our problem becomes obvious. We must use systems techniques to evaluate genotypes of cattle in different environments to establish as an objective the optimum type of bulls, cows and calves for a given environment. We can then use research information to identify breeds or breed types available and determine the best way through selection or crossbreeding to get to the optimum.

In summary, I have tried to answer the five questions that I first posed. We started with a large, wild Bos primigenius that was domesticated in several areas of Europe, Asia and North Africa more than 5000 years ago. We got to where we are now by methodical, unconscious and natural selection for many characteristics in many environments. We have now a population that is heterogeneous and poised to respond to selection in just about any direction we want to go. We must be careful, however, not to select haphazardly and ignore the entire biology of the animals and the plants they eat. With modern systems analysis techniques, we can determine where it is we want to go within a given environment and use established selection and crossbreedding techniques to get there. In the meantime, we must continue our research on the biology of the animals and on genetic interactions within them and on genotype-environment interactions on our varied rangelands.

Literature Cited

Cole, L. C. 1954. The population consequences of life history phenomena. Quart. Rev. Biol. 29:103.

Darwin, Charles. 1897. The Variation of Animals and Plants Under Domestication. Appleton & Co., New York.

Dobzhansky, Theodosius. 1970. Genetics of the Evolutionary Process. Columbia Univ. Press, New York.

French, M. H., I. Johansson, N. R. Joslin and E. A. McLaughlin. 1966. European Breeds of Cattle. FAO Agricultural Studies, No. 67.

Giesel, J. T. 1974. Fitness and polymorphism for net fecundity distributions in iteroparous populations. Amer. Nat. 108:321.

Haldane, J. B. S. 1954. The measurement of natural selection. Proc., 9th Int. Cong. of Genetics 1:480.

Herre, W. 1958. Abatammung und Domestikation der Haustiere. Handbuch der Tierzuchtung 1:1-58.

Mason, I. L. 1973. The role of natural and artificial selection in the selection in the origin of breeds of farm animals. A critique of Darwin's 'The variation of animals and plants under domestication'. Z. Tierzuchtg. Zuchtgsbiol 90:229.

Sadlier, R. M. F. S.   1969.   The Ecology of Reproduction in Wild and
    Domestic Mammals. Methuen & Co., Ltd., London.

Spencer, Herbert. 1897. Principles of Biology. Appleton & Co., New York.

Wright, Sewall. 1978. The relation of livestock breeding to the theories
    of evolution. J. Anim. Sci. 46:1192.

THE EVOLUTION OF RANGE PLANTS

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Introduction

Twenty-five years ago, Hutchinson (1959) posed one of the more intriguing questions that a biologist can address in his essay "Homage to Santa Rosalia." In essence, he wondered "Why are there so many kinds of plants and animals?" Such a theme, of course, has been indirectly addressed in discussions on evolution both before and after the paper, but Hutchinson succeeded in focusing attention on the paradox of how relatively finite physical resources engender such a wide array of living organisms. Among ecologists and resource managers this concern is highly germane to understanding community structure and function since the kinds and numbers of species that are present is one of the most basic qualities of natural communities.

During the past two decades, knowledge of genetics, ecology and evolution has expanded to the point where interdisciplinary approaches have been fruitful in merging principles from each. Books by Brussard (1978) and Merrell (1981) are but two examples of this trend. Evolutionary principles discussed by Mayr (1963), Stebbins (1950) and others have been examined, as pointed out by Levin (1978), in light of empirical studies on intraspecific competition (Harper and White, 1970; 1974), dynamics of succession and colonization (Yarranton and Morrison, 1974), safe site specificity (Harper, 1961, 1965; Sheldon, 1974), and the dynamics and longevity of the seed pool (Harrington, 1972; Roberts, 1972). In addition, theoretical consideration of plant population ecology has directed attention to life history strategies with particular emphasis on seed dormancy (Cohen, 1967; 1968), seed dispersal (Gadgil, 1971; Roff, 1975), reproductive schedules (Levins, 1968; Cohen, 1971; 1976; Bradshaw, 1974; Schaffer, 1974a, b) and longevity (Gadgil and Bossert, 1970; Gadgil and Solbrig, 1972; Kawano, 1975; Schaffer and Gadgil, 1975). Demographic attributes that have been discussed in the same fashion include: population growth with density-dependent regulation (Charlesworth and Giesel, 1972; Charlesworth 1971, 1973), age-specific selection (Anderson, 1971; King and Anderson, 1971), and migration (Jain and Bradshaw, 1966; Antonovics, 1968; Gillespie, 1974, 1975, 1976; Bullock, 1976; Nagylaki, 1976). Although these papers and others illustrate the convergence of ecology and genetics with evolutionary theory, these fields remain, in most respects, separate disciplines. Moreover, many structural and functional characteristics of individual plant species have not been examined in either context. For this reason, it is appropriate to discuss some of the factors that affect evolutionary processes in range plant communities.

The objective of this paper has been to identify and discuss aspects of the evolutionary process that relate to the symposium theme with particular reference to environmental considerations and more specifically to the response of plant species. Discussion is centered around general plant responses, but

emphasis is directed toward range plant species when appropriate. In surveying the published literature, attention has been directed primarily toward reviewing material from the past two decades. Although earlier work certainly merits consideration, it has been necessary to place some limitations on the amount of material that can be included. Detailed discussion on the principles and mechanisms of evolution are beyond the scope of this paper. For this information, the interested reader is referred to the work of Stebbins (1950), Mayr (1963) or any of the other general evolutionary theorists.

Although many topics merit in-depth discussion, four have been selected for more detailed consideration. They are: (1) factors differentiating animals from plants, (2) important elements of plant life history, (3) environmental constituents that operate in the selection and evolutionary process, and (4) plant adaptations.

Evolutionary Factors Distinguishing Animals From Plants

When comparisons are made between animals and plants with respect to evolution, it is obvious that there are many similarities. Factors such as crossing over, linkage, mutation and other cytological processes are common to each. However, there are also several differences which have a bearing on the evolutionary process (Stebbins, 1950; Mayr, 1963). Three, in particular, seem directly related to evolution in range plants.

First, the complexity of development is greatly different between animals and plants. Animals have developed tissue and organ systems which relate to one another in a far more intricate way than do the organ systems of plants. Tissue systems in a cow or fruit fly, for example, are far more complex than those that might be found in a sagebrush or grass plant. The implication of this is that single mutations in animals can have a much more devastating and sometimes lethal impact unless they are able to function harmoniously among the different organ systems. In contrast, single mutations in plants are far less disruptive because the need for precise integration among the different organ systems is seldom as critical. This means that single mutations in plants can play a more active role in the evolutionary process. It also suggests that gene systems in plants are perhaps more broadly based than they are in animals.

The second major difference between plants and animals is that the longevity and capacity for asexual development in plants is considerably greater than that in animals. When the lifespan of animals is considered, it is rather unusual to find an animal that is reproductively active for more than 5 or 10 years; and it is truly exceptional to find an animal that is reproductively active for more than 100 years. Plants, in contrast, commonly live scores of years, and in many cases hundreds and even thousands of years. The most common examples of such plants are perhaps redwood trees and bristlecone pines which are well known to achieve ages of thousands of years. However, even among grasses and shrubs, great longevity is common if it is thought of in terms of survival of individual genotypes. In fact, among the grasses, Hitchcock and Chase (1931) have estimated that many buffalo grass plants on the western plains have been living there since the retreat of the glaciers. The crucial difference between groups then is that animals use the sexual process for two purposes: first, in reproducing the species as such; and

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secondly, in achieving genetic recombination. Plants, in contrast, do not have to depend solely upon sexual reproduction to insure the survival of the species. Instead, they use it primarily for achieving genetic recombination. In addition, the great longevity of many genotypes provides an opportunity for considerably more evolutionary experimentation, and this can create populations that are more highly adapted to individual environmental conditions. Thus, ecotypic differentiation within a plant population seems to be a common phenomenon.

A third major difference between plants and animals has to do with mobility. Obviously animals are more mobile than plants. If environmental conditions are not suitable, animals can move to a different environment. They, thus, become more independent of the environment. In addition, animals also move to achieve reproductive success; whereas in plants, this is largely a passive process. The consequence of reduced mobility in plants is that there must be a premium placed on storing genetic variability in the population. This insures that at least some individuals within the population will be guaranteed success. It also means that individuals within the population will generally have to rely on production of large amounts of seed, and it may mean that plants exhibit more phenotypic plasticity than do animals.

To recapitulate the differences between animals and plants, it is reasonable to recognize at least two common evolutionary strategies. First, an organism might become better adapted to the environment. This strategy is probably best represented by plants. Secondly, an organism can become relatively independent of the environment. This strategy is more commonly employed among animal species.

Life History of Plants

Although the life history of most vascular plants can be highly complex, it can also be considerably simplified by representing individual aspects of a plant's reproductive life cycle. This has been illustrated in Figure 1. An individual plant starts out as a member of the seed pool. In the seed pool, it may remain for a period of weeks, months or, in some cases, several years. Eventually, the seed will germinate and become established as it grows and survives to reproductive maturity. At that point, the primary function of the genotype is to produce pollen or ovules that can be used in recombining genetic material into new seeds. These new seeds then go back into the seed pool.
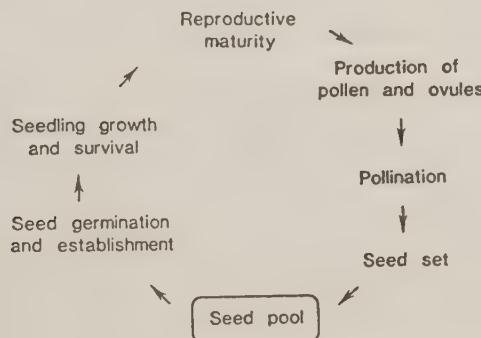
Figure 1. Schematic representation of selected stages in the general life history of a plant.

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From an evolutionary standpoint, at least 95% of the selection which is going on in plants takes place with respect to seed germination, seedling growth, and early seedling survival (Hickman, 1979). Only 5% of the selection involves plants that are reproductively mature. For this reason, selection among mature plants can be considered almost incidental although certainly when adaptations to the environment are considered they usually refer to mature plants. Because of the importance of seed germination and seedling growth in the evolutionary process, it is appropriate to direct attention primarily toward this part of the life history of a plant. One of the most noteworthy characteristics of plants is the number of seeds that are produced. People have known for a long time that plants produce a great abundance of seed, as witnessed by the Bible quotation "Some seeds fell by the wayside, some fell upon stony places, some fell among thorns, but others fell into good ground (The Bible, St. Mathews, Chapter 13)". While prolific seed production has been recognized for some time it has only been within the last 15 to 20 years that the importance of the high production of seeds has been realized.

Cavers (1983) has reviewed recent literature on seed demography, and he notes that there are at least five important roles or functions of a large number of seeds. First, there must be a lot of seeds available so that at least a few can be dispersed to new areas. Seed distribution patterns around a parent plant typically show that most seeds tend to fall under or near the parent. Even among light seeds that are wind-dispersed, the greatest concentration occurs only a short distance from the parent. Therefore, dispersal relationships are best described as a seed shadow which decreases as a negative exponential function of the distance from the parent plant (Bullock, 1976). The consequence of this type of relationship is that migration of adapted genotypes is limited by the number of seeds. The greatest potential exists among plant species that are prolific seed producers.

A second reason for a large number of seeds is to occupy all potential microsites in the immediate vicinity of the parent plant. Harper (1977) has pointed out that there are only a small number of potential safe-sites where an individual seed (i.e., genotype) can germinate and grow to maturity. Each safe-site, therefore, presents a potential opportunity for a plant to become established. Because of the passive distribution of seeds in most species, it becomes important that a large number of seeds be produced so that at least some will reach their safe-site. Another factor recognized by Cavers (1983) is that the flower, seed and young seedling are small and often fragile life forms that can be readily destroyed by adverse weather, predators or parasites. If seeds or seedlings are present in large numbers, there is a greater chance that a few will survive; whereas if only a few individuals are present, they could all be destroyed.

A third reason for large seed numbers is that survival during unfavorable periods is facilitated. Many habitats, and particularly those associated with rangelands, have adverse weather conditions for extended periods. Factors such as extreme temperatures (low or high), drought, and fire regularly occur and can reduce populations of seeds, seedlings and mature plants. To compensate for environmental extremes, many species are adapted to survive adverse periods as seeds. When seeds are abundant in the seed bank, the probability of surviving long, unfavorable periods is increased. This has been reported by Schafer and Chilcote (1970) in response

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to soil temperature and moisture, and it has been discussed by Roberts (1981) in a more general review.

Population dynamics within seed banks are strongly dependent upon the life history of individual species (Cavers, 1983). Those species which possess more than one mechanism for survival are not as dependent on the seed bank. Long-lived perennial species, for example, may have temporary seed banks; whereas, related species that are shorter-lived may have more persistent seed banks (Weaver and Cavers, 1979). Another reproductive strategy used by some short-lived range plants is to vary their growth form and seed production according to prevailing environmental conditions. Bromus tectorum, for example, is able to survive and thrive under variable moisture conditions on the same site as an ephemeral, a summer annual, and a winter annual (Mack and Pyke, 1983). This characteristic has obvious survival advantages in annual species, but similar responses also occur in many perennial species in which large numbers of seeds may be produced at one time to compensate for years when seed production is unsuccessful.

A fourth function of prolific seed production is to enable some seeds to survive the impact of herbivores, granivores, and pathogens. If a species is to succeed in sexual reproduction, it must produce sufficient seeds to overcome both the indirect and direct effects of such organisms. Reduction of photosynthetic tissue by defoliation usually results in decreased seed production (Harper et al., 1970; Cavers, 1973). Since grazing by ungulates and insect herbivores is common on rangelands, most plant species have made compensatory adjustments under these circumstances. In contrast, direct consumption of seeds by either granivores or pathogens may have a substantial effect on the reproductive capacity of some species but little effects on others (Reed and Stephenson, 1972). Moreover, the response within a single species can be influenced by environmental conditions such as plant density (Lee and Bazzaz, 1980). Because of the complexity of such interactions, large numbers of seeds are often necessary to overcome the collective effects of seed destruction.

The fifth, and certainly an obvious, reason for high seed production is to facilitate the recruitment of new genotypes into the population. Because environmental conditions are not stable forever, it is crucial that new, better-adapted genotypes be added to the base population. Cavers (1983) has suggested that this process is more easily accomplished when larger numbers of seeds exist. He surmises that as the numbers of seeds increase, the probability also increases that a more successful new genotype will be added to the population. As a consequence, there will be a greater number of new genotypes available even though most of them are probably not well adapted and may die at a seed or seedling stage (Templeton and Levin, 1979).

Understanding the life history of plants is critical to understanding how they have evolved to meet environmental demands. Certainly range plants are no exception. Since seeds and seedlings play such an important role in plant population dynamics, discussion in this section of the paper has focused upon seed demography. However, the environmental conditions under which plants evolve is also a major factor in determining aspects of their life history.

Plants exist in a complex environment that fluctuates with respect to both space and time. Basic elements of this complexity have been presented by Billings (1964) in a succinct, yet thorough, discussion of environmental components. When considering a plant's response to environmental conditions, it is important to recognize both vertical and lateral gradients existing within the soil and atmosphere. These define individual microsites, each with its own microclimate. Moreover, environments fluctuate over time on a diurnal and annual basis as well over more extended intervals. Plants must adapt to these conditions to be evolutionarily successful.

In some situations, environmental constituents can best be classified as consisting of either physical or biological components. Such an approach is often productive when delineating factors of major ecological importance to an organism or when attempting to explain the concept of limiting factors. However, it should also be realized that a classification scheme of this sort has limitations and represents an oversimplification. In reality, it is difficult, if not impossible, to isolate or change one part of the environment without affecting other parts (Billings, 1964). Interactions and interrelationships among environmental components are ultimately inseparable. When considered through time, they form an essential ingredient of evolutionary development.

Individual elements of the environment are best thought of as being dynamic. That is, they change through time in response to cyclic (diurnal or annual) and cumulative changes in other elements. The nature of this relationship was first described by Friederichs (1927) and later refined by Billings (1952) in the development of the holocoenotic concept. In discussing evolution of range plants, it seems most workable to reduce the number of environmental variables to five. These are illustrated in Figure 2.
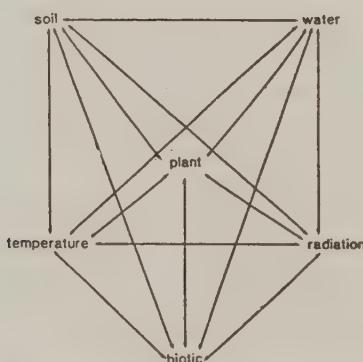
Figure 2. Diagramatic representation of holocoenotic interactions among environmental factors. Arrows reflect nature of two-way interactions between factors. Modified from Billings (1952) and presented in simplified form.

Radiation can be regarded as the primary driving force regulating energy capture and flow in terrestrial ecosystems. Light energy controls photosynthesis and is of considerable importance in the heating of the environment. Radiation can fluctuate according to: (1) the intensity or amount per unit

time, (2) the quality or wavelength composition, and (3) photoperiod or duration. In range ecosystems, radiation amounts are generally high. Vegetation is usually sufficiently sparse so that there is less light attenuation than in other ecosystems. As a result, wavelength composition usually does not deviate greatly from local solar values. However, rangelands are widely distributed across many latitudes and altitudes, and this can cause striking differences in wavelength composition and photoperiod when comparisons are made from widely separated sites.

Temperature relationships are important in regulating physiological responses of plants, and they can affect plant distribution on both a local and regional basis. Temperature gradients commonly exist in both the atmosphere and soil that are affected by type of plant cover; soil texture, moisture content, and albedo; altitude; topography; slope and other factors. As a result, microenvironments often are present that can have a strong influence on seed germination, seedling growth and performance in mature plants. Because range ecosystems extend over wide geographic areas, however, range plants have become adapted to a wide variety of temperature regimes. It seems unlikely, therefore, that unique temperature responses would be expected among range plants as a group.

Water is one of the most important factors in determining distribution patterns and density in plant species. In addition, it has a direct bearing on plant productivity and reproductive potential of most species. The amount, frequency and type of precipitation usually determines how much effective moisture is present in the soil and available for plant growth. However, factors such as runoff, texture and depth of the soil, organic matter, vegetation interception, transpirational activity, temperature, humidity and many other variables can have an enormous impact on how much precipitation is retained. Range plants, in general, are found in areas of limited moisture. As a result, evolutionary pathways for surviving xeric conditions have probably been more thoroughly explored among range plants than in plants from other ecosystems. Specific adaptations and examples will be discussed in the subsequent section.

Soils function as a reservoir for water and minerals in the ecosystem. In addition, they provide physical support for plants. As an environmental factor, soil is extremely complex in its effects, and it can be regarded as a physical-biological system that is at least as complex as the vegetation above it (Billings 1964). Variations commonly exist with respect to texture, structure, chemistry and biological attributes that can affect plant response. With respect to evolution in range plants, soils have undoubtedly played an important role. However, it is difficult to identify specific adaptations that can be closely associated with soil properties. This can be attributed, in part, to the wide diversity in rangeland soils, but it is probably also a function of how closely both soils and plants are attuned to climatic conditions.

Biotic interactions often have a substantial effect on both the structure and function of individual plants, populations and ecosystems. From a plant perspective, two types of interactions can be recognized: plant-plant and plant-animal. Both are extremely common. Plant-plant interactions have usually been considered in terms of competition for limited resources such as

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water, minerals or space. Competition of this sort can be either inter- or intra-specific, and it generally tends to produce both structural and functional diversity in most vegetation types (Billings, 1964). Considerable literature on plant competition has appeared that has direct and indirect implications on plant evolution. Much of this has been summarized by Harper and White (1970; 1974). Plant-animal interactions assume importance in many ecosystems, but they are perhaps most noticeable in adaptations and responses of range plants. The principle role that animals play with respect to plants is that of eating or otherwise damaging them, and this has been described in detail by Crawley (1983). Other important roles that animals play in plant-animal interactions include pollination and mineral cycling. In a variety of ways, therefore, animals can make a key contribution to the environment of plants. Individual adaptations to biotic influences are discussed in the following section.

Plant Adaptations

There are a multitude of individual adaptations that could justifiably be considered in relation to environmental conditions. Indeed, entire volumes have been written on plant adaptations in the context of evolutionary theory. An in-depth review of this literature will not be included in my paper. It would probably be more instructive to consider a few of the important adaptations range plants have made to their environments. Specifically, it seems most appropriate to focus upon water and biotic factors. From the perspective of a range plant, these two probably have exerted more influence than the factors of radiation, temperature and soil that were discussed previously.

Plants, in general, have evolved at least three different life forms in response to limited water supply. First, they can be ephemeral or short-lived annuals that escape limited water by completing their growth cycle very rapidly. They then survive adverse conditions as a seed. These plants have relatively large shoots in proportion to their small root systems (Daubenmire, 1967). Typically, ephemerals are abundant in arid regions. When rainfall occurs, seeds germinate and quickly grow to maturity. Seed is then set before the soil dries out to the depth of their small root systems.

Succulents represent a second life form that is well adapted to limited water on rangelands. These plants characteristically have numerous parenchyma cells with enlarged vacules for storing water (Daubenmire, 1967). Root systems may be shallow, but widespread horizontally, so that water can be rapidly extracted from the soil when rainfall occurs. Some species have fine rootlets that are drouth-deciduous and will be present only when soil moisture conditions are favorable. Succulents survive limited water primarily through their ability to store water when it is present and retain it for extended periods. Adaptations that are helpful in this regard include: loss of true leaves (e.g. cactus), thick cuticular layers, reduced numbers of stomates, sunken stomates, and nighttime incorporation of CO_2 (e.g., crassulacean acid metabolism).

A third category of life form commonly found in range plants is the nonsucculent perennial. This group includes the majority of range plants that are able to thrive with limited amounts of water. Daubenmire (1967) has presented a good summary of some of the morphological and physiological adaptations that

are often present in this group of plants. Frequently, these plants have tap roots that elongate rapidly as a seedling. This enables seedlings to keep ahead of progressive desiccation from the surface down, and it allows them to become established after short periods of precipitation. Plants may then develop extensive root systems in proportion to shoot systems, and it is not unusual to find 75% or more of the plant growth underground. Plants in this group may have high osmotic pressures in the plant cells, and this characteristic perhaps enhances their ability to endure desiccation. In addition, many range plants are able to reduce transpiration to low levels, especially under conditions of water stress or permanent wilting. This is accomplished by shedding leaves, becoming dormant, or developing epidermal characteristics such as cuticle, wax or pubescence. Another adaptation that can occur in perennial xerophytes is a reduction in leaf and/or cell size. Although the role that is played by this adaptation remains obscure, the phenomenon is sufficiently common to conclude that it fulfills a fundamental function. Daubenmire (1967) has suggested that reduction in size reduces the likelihood of drouth necrosis during dehydration. It may also help keep leaves from overheating when exposed to strong solar radiation. Not all of the characteristics described above will occur in any one plant, but certainly they are very common in range plants that grow under conditions of limited moisture. Each species has solved its water-balance problem with a unique combination of adaptive characteristics. This combination, moreover, may be entirely different than an adjacent species subjected to similar water stresses.

The last type of adaptation that will be discussed is that of adaptations to biotic components of the environment. Specifically, attention needs to be directed toward interactions between animals and plants. From this perspective, it is important to recognize that animals generally eat plants as a source of energy. They will particularly concentrate on seeds for this purpose. Plants, in contrast, will develop a variety of mechanisms that help them avoid utilization by animals or, in some cases, take advantage of this utilization. Interactions of this sort are generally regarded as having involved coevolution of both organisms. The subject of coevolution, however, is a complex one, and the process may indeed comprise much of evolution. Recent books by Thompson (1982), Futuyma and Slatkin (1983) and Nitecki (1983) discuss the topic in considerable detail, and the interested reader is encouraged to consult them. Two aspects of coevolution that will receive attention here are: (1) the importance of animals in plant reproduction and (2) defense mechanisms found in plants. Both commonly occur in range plants.

Animals play an important role in the reproductive success of many plants. They do this primarily by participating in pollination and seed dissemination. Plants have evolved flowers that are different shapes, sizes and colors. Such differences are designed to take advantage of the many animal pollinators that are present in the environment. Some examples would include insects such as bees, flies, butterflies, moths and beetles. It would also include certain birds such as hummingbirds and a few mammals such as bats. Animals also play an active role in seed dissemination, and seeds have evolved a variety of adaptations to facilitate animal transport. For example, there are various clinging devices whereby seeds or fruits can latch onto the feathers and fur of animals as they pass. The cocklebur is a classic example, and there are many others. Another common adaptation is that of a thickened seed coat. This allows a seed to pass through an animal's digestive tract and germinate

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after it has been transported to a different location. In conjunction with this, fruits may have evolved a highly palatable pericarp that entices animals to consume seeds.

A number of defense mechanisms have evolved in plants in response to herbivory. In range plants, adaptations of this sort seem particularly important because plants may be subjected to utilization from several classes of herbivores. For example, grasses are commonly eaten by ungulates, insects (e.g., grasshoppers), nematodes and others. Defense mechanisms can be classified into morphological, chemical or physiological adaptations depending upon the primary means of defense. Most plants that are commonly eaten employ more than one line of defense, and this may vary according to the individual plant part.

The development of thorns can be interpreted as a morphological adaptation to grazing. They are often present in areas where there has been a long history of grazing. On the plains of Africa, for example, where traditionally there have been large herds of grazing animals, thorns are found on most shrubs. In contrast, thorns are very uncommon on Australian or New Zealand shrubs, where grazing pressure has been considerably less. A second adaptation to herbivory is morphological modifications of the epidermis. At least two adaptations -- thickening of the cuticular layer and the presence of epidermal hairs -- can function to limit access by insect herbivores. A third example of a morphological adaptation would be the location of meristematic tissues in plants. In grasses, for example, the meristematic tissue is located low to the ground and in some species below ground. Such plants, therefore, are relatively resistent to grazing pressure because they can readily regrow from such meristematic tissue.

Chemical adaptations to herbivory include both the formation of secondary plant compounds and perhaps a reduction in herbage quality. Secondary compounds such as terpenoids are high energy molecules that seem to serve little apparent function in many plants. However, they frequently reduce palatability to herbivores, and they might be interpreted, therefore, as a grazing defense mechanism for the plant. Likewise, a decrease in forage quality, as exemplified by lower digestibility or protein content and higher silica or lignin content, may have no direct relationship to plant function. Changes such as these could be interpreted as another chemical defense mechanism for the plant since they will ordinarily decrease the amount of grazing to which a plant is subjected.

Physiological adaptation also appears to be a common way that plants have adjusted to herbivory. In some situations, plants have evolved under conditions of continuous high utilization, and they apparently have acquired physiological tolerance to heavy and/or frequent defoliation. In essence, they simply endure or persist under these conditions with minimal negative effects on growth or reproductive potentials. Crested wheatgrass is an example of this sort of plant. Another physiological adaptation that may be related to herbivory is the phenological development and growth habit of some plants. For example, dormant periods and/or carbohydrate storage cycles may occur in such a fashion that plants simply escape harmful grazing when it is most severe (e.g., when insect or other animal populations are high). Such a strategy would be expected to have minimal impact on a plant.

Summary

In summary, my paper has identified and discussed some of the factors that are important in the evolution of range plants. Specific topics that were addressed include: (1) factors differentiating animals from plants, (2) elements of a plant's life history, (3) environmental considerations, and (4) plant adaptations. Certainly there is much ground left unplowed, but I have attempted to discuss some of the more important aspects in each of these subject areas.

Literature Cited

Anderson, W. W. 1971. Genetic equilibrium and population growth under density-regulated selection. Amer. Natur. 105:489-498.

Antonovics, J. 1968. Evolution in closely adjacent populations. VI. Manifold effects of gene flow. Heredity 23:507-524.

Billings, W. D. 1952. The environmental complex in relation to plant growth and distribution. Quart. Rev. Biol. 27:251-265.

Billings, W. D. 1964. Plants and the ecosystem. Wadsworth Publishing Co., Belmont, Calif. 154 p.

Bradshaw, A. D. 1974. Environment and phenotypic plasticity. Brookhaven Symp. Biol. 24:75-94.

Bullock, S. H. 1976. Consequences of limited seed dispersal within a simulated annual population. Oecologia 24:247-257.

Brussard, P. F. (Ed.) 1978. Ecological genetics: The interface. Springer-Verlag, New York. 247 p.

Cavers, P. B. 1983. Seed demography. Can. J. Bot. 61:3578-2590.

Cavers, P. B. 1973. The effects on reproduction of removal of plant parts by natural or artificial means. In: Proceedings of 2nd International Symposium on Biological Control of Weeds. Commonw. Inst. Biol. Control Misc. Publ. No. 6:140-144.

Charlesworth, B. 1971. Selection in density-regulated populations. Ecology 52:469-475.

Charlesworth, B. 1973. Selection in populations with overlapping generations. V. Natural selection and life histories. Amer. Natur. 107:303-311.

Charlesworth, B. and J. T. Giesel. 1972. Selection in populations with overlapping generations. II. Relations between gene frequency and demographic variables. Amer. Natur. 106:388-401.

Cohen, D. 1967. Optimising reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. J. Theoret. Biol. 16:1-14.

Cohen, D. 1968. A general model of optimal reproduction in a randomly varying environment. J. Ecol. 56:219-228.

Cohen, D. 1971. Maximizing final yield when growth is limited by time or by limiting resources. J. Theoret. Biol. 31:299-307.

Cohen, D. 1976. The optimal timing of reproduction. Amer. Natur. 110:801-807.

Crawley, M. J. 1983. Herbivory: The dynamics of animal-plant interactions. University of California Press. 437 p.

Daubenmire, R. F. 1967. Plant and environment. John Wiley & Sons, New York. 422 p.

Friederichs, K. 1927. Grundsatyliches uber die Lebenseinheiten hoherer Ordnung und den okolgischen Einheitsfaktor. Naturwissenschaften 15:153-157, 182-186.

Futuyma, D. J. and M. Slatkin (Eds.) 1983. Coevolution. Sinauer Associates. 555 p.

Gadgil, M. 1971. Dispersal: Population consequences and evolution. Ecology 52:253-261.

Gadgil, M. and W. Bossert. 1970. Life history consequences of natural selection. Amer. Natur. 104:1-24.

Gadgil, M. and O. T. Solbrig. 1972. The concept of r- and K- selection: evidence from wild flowers and some theoretical considerations. Amer. Natur. 106:14-31.

Gillespie, J. H. 1974. Polymorphism in patchy environments. Amer. Natur. 108:145-151.

Gillespie, J. H. 1975. The role of migration in the genetic structure of populations in temporally and spatially varying environments. I. Conditions for polymorphism. Amer. Natur. 109:127-135.

Gillespie, J. H. 1976. The role of migration in the genetic structure of populations in temporally and spatially varying environments. II. Island models. Theoret. Pop. Biol. 10:227-238.

Harper, J. L. 1961. Approaches to the study of plant competition. Symp. Soc. Exp. Biol. 15:1-39.

Harper, J. L. 1965. Establishment, aggression, and cohabitation in weedy species. In: H. G. Baker and G. L. Stebbins (Eds.) The Genetics of Colonizing Species pp 243-265. Academic Press, New York.

Harper, J. L., P. H. Lovell, and K. G. Moore. 1970. The shapes and sizes of seeds. Ann. Rev. Ecol. Syst. 1:327-356.

Harper, J. L. and J. White. 1970. The dynamics of plant populations. Prov. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek) 41-63.

Harper, J. L. and J. White. 1974. The demography of plants. Ann. Ecol. Syst. 5:419-463.

Harper, J. L. 1977. Population Biology of Plants. Academic Press, New York.

Harrington, J. F. 1972. Seed storage and longevity. In: T. T. Kozlowski (Ed.) Seed Biology 3:145-245. Academic Press, New York.

Hickman, J. C. 1979. The basic biology of plant numbers. In: O. T. Solbig, S. Jain, G. B. Hohnson, and P. H. Raven (Eds.). Topics in plant population biology. pp 232-263. Columbia Univ. Press, New York.

Hitchcock, A. S. and A. Chase. 1931. Grass. In old and new plant lore. Smithsonian Science Series 11:201-250.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or Why Are There So Many Kinds of Animals? Amer. Nat. 93:145-159.

Jain, S. K. and A. D. Bradshaw. 1966. Evolutionary divergence among adjacent plant populations. I. Evidence and its theoretical analysis. Heredity 21:407-441.

Kawano, S. 1975. The productive and reproductive biology of flowering plants. II. The concept of life history strategy in plants. J. Coll. Liberal Arts, Toyama Univ. 8:51-86.

King, C. E. and W. W. Anderson. 1971. Age-specific selection II. The interaction between r- and K- during population growth. Amer. Natur. 105:137-156.

Lee, J. D. and F. A. Bazzaz. 1980. Effects of defoliation and competition on growth and reproduction in the annual plant Abutilon theophrasti. J. Ecol. 68:813-321.

Levin, D. A. 1978. Some genetic consequences of being a plant. In P. F. Brussard (Ed.) Ecological Genetics: The Interface. pp 189-212. Springer-Verlag, New York.

Levins, R. 1968. Evolution in Changing Environments. Princeton Univ. Press, New Jersey.

Mack, R. N. and D. A. Pyke. 1983. The demography of Bromus tectorum: variation in time and space. J. Ecol. 71:69-93.

Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge. 797 p.

Merrell, D. J. 1981. Ecological genetics. University of Minnesota Press, Minneapolis. 500 p.

Nagylaki, T. 1976. Dispersion-selection balance in localized plant popula-
tions. Heredity 37:59-67.

Nitecki, M. H. (Ed.). 1983. Coevolution. University of Chicago Press.
392 p.

Reed, F. C. and S. N. Stephenson. 1972. The effects of simulated herbivory
on Ambrosia artemisiifolia L. and Arctium minus Schk. Mich. Acad.
4:359-364.

Roberts, E. H. 1972. Viability of Seeds. Chapman & Hall, London.

Roberts, H. A. 1981. Seed banks in soils. Adv. Appl. Biol. 6:1-55.

Roff, D. A. 1975. Population stability and the evolution of dispersal in a
heterogeneous environment. Oecologia 19:217-237.

Schafer, D. E. and D. O. Chilcote. 1970. Factors influencing persitence and
depletion in buried seed populations. II. The effects of soil tem-
perature and moisture. Crop Sci. 10:342-345.

Schaffer, W. M. 1974a. The evolution of optimal reproductive strategies: The
effects of age structure. Ecology 55: 291-303.

Schaffer, W. M. 1974b. Optimal reproductive effort in fluctuating environ-
ments. Amer. Natur. 108:783-790.

Schaffer, W. M. and M. D. Gadgil. 1975. Selection for optimal life histories
in plants. In: M. Cody and J. Diamond (Eds.) Ecology and Evolution of
Communities. pp 142-157. Harvard Univ. Press, Cambridge, Massachusetts.

Sheldon, J. C. 1974. The behavior of seeds in soil. III. The influence of
seed morphology and the behavior of seedlings on the establishment of
plants from surface-lying seeds. J. Ecol. 62:47-66.

Stebbins, G. L. 1950. Variation and evolution in plants. Columbia University
Press, New York. 643 p.

Templeton, A. R. and D. A. Levin. 1979. Evolutionary consequences of seed
pools. Amer. Nat. 114:232-249.

Thompson, J. N. 1982. Interaction and coevolution. Wiley-Interscience.
179 p.

Weaver, S. E. and P. B. Cavers. 1979. Dynamics of seed populations of Rumex
crispus and R. obtusifolius (Polygonaceae) in disturbed and undisturbed
soil. J. Appl. Ecol. 16:909-917.

Yarranton, G. A. and R. G. Morrison. 1974. Spatial dynamics of a primary
succession: Nucleation. J. Ecol. 62:417-428.

RANGE RESOURCE MANAGEMENT AND POTENTIAL

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Rangelands historically have provided the forage base for livestock production in the western states. As the West was settled, the need for meat was supplied from the western rangelands. In the late 1800's, it became apparent that the massive forage base provided from the western range was well suited to beef production and large investments were made in developing a cattle population to exploit the resource. This cattle population was not managed to utilize the forage on a sustained basis and a rapid deterioration in overall productivity followed. The deterioration of the western rangelands was recognized and legislation to begin control of grazing was implemented in the early 1900's, culminating in the Taylor Grazing Act of 1934 that put all public lands under management administered by the federal government. While only half of the western range is administered by the government, the situation on federal lands reflects similar problems that had occurred on public lands.

The deterioration of the forage base in the West was coupled with an evolution of the livestock industry. Controls of grazing on public lands largely eliminated the itinerant livestock herds and forced livestock owners to operate from a base property. The long-term effect was to establish ranches with a private land base that grazed their livestock seasonally on public lands or private ranches that had no access to forage on public lands. These constraints were coupled with increasing abilities to grow forage crops to supplement the rangeland forage base.

At the same time, a large irrigated agricultural cropping program was developed in the western states through extensive dammings of rivers and development of irrigation systems. This not only produced crops sold for direct human consumption and forages for livestock but also a tremendous volume of by-products and aftermath that was suitable for livestock consumption.

As a result of several factors such as federal and state laws and policies, development of irrigation systems and increased understanding of agricultural technology and forest harvest, the present cattle industry in the West has increased use of forages other than range forage. Bedell and Stringham (1984) surveyed ranchers in eastern Oregon to define forage sources on ranches with public land grazing permits (table 1). Their survey indicated about half of the forage used annually was from rangeland. Hay provided nearly a third of the forage used each year. These results from Oregon generally reflect the current situation in the western states, though no similar surveys have been made in other areas in recent years. The continually increasing costs of farming are forcing ranchers to reduce cash inputs. This has resulted in an interest to increase rangeland grazing use. The question is, can the rangelands of the West, still deteriorated from historical abuses, support an increased intensity of grazing? To answer this question, we need to evaluate the current state of productivity and then look to potentials for increased stocking.

TABLE 1. SEASONAL FORAGE SOURCES FOR EASTERN OREGON CATTLE RANCHES WITH PUBLIC LAND GRAZING PERMITS

Source	Percent
BLM	12
USFS	8
Private range	28
Other range	1
All range	49
Irrigated pasture	10
Aftermath	9
Hay	32

Source: Bedell and Stringham, 1984.

Rangeland Productivity. Rangelands and forests are the dominant kinds of land in the western states making up over 8 million acres (table 2). Over 80% of this land area is grazed. About 1.5 million acres are not grazed because of dense forests or various kinds of reservations for other uses. The large input to forage supply in the West from range of about 350 million tons (table 3) is due to the extensive area involved.

TABLE 2. RANGE AND FOREST IN 17 WESTERN STATES IN 1000 ACRES

	Grazed	Ungrazed	Total
Western	504,002	117,669	621,671
Plains	185,106	28,746	213,852
Total	689,108	146,415	835,523

Source: USDA-Forest Resource Report No. 19.

TABLE 3. HERBAGE AND BROWSE PRODUCTION IN 17 WESTERN STATES

Western	197 million tons
Plains	155
Total	352

Source: USDA-Forest Resource Report No. 19.

Current grazing intensities vary by the kind of range and grazing management program (table 4). Mountain meadows are the most productive because of good moisture status and dependable climate. Grasslands are well adapted to grazing and reflect generally high animal production. Rangelands with extensive populations of woody plants, either shrubs or trees, are currently quite low in production of livestock forage.

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TABLE 4. LIVESTOCK PRODUCTION BY ECOSYSTEM

Sagebrush	8.00 acres/AUM
Desert shrub	33.00
Pinyon-juniper	20.00
Mountain grasslands	3.50
Mountain meadows	.85
Ponderosa pine	14.00
Shortgrass prairie	3.20
Tallgrass prairie	1.00

Source: USDA-Forest Resource Report No. 19.

Grazing management approaches vary from low intensity of management to extremely intensive approaches. Much of the rangeland in the West is stocked at levels to support cattle under continuous grazing. This may be for a grazing season or yearlong where climate permits. When properly stocked, this system of grazing is productive of livestock and sustainable over time. Since plants vary seasonally in sensitivity to defoliation, a variety of rotation systems have been developed, largely to enhance range condition. Timing grazing to occur on part of the range after flowering, usually in alternate years, is called deferred rotation grazing. This approach is common on rangelands where a principal objective is improvement in range condition. Of the variety of rotation grazing systems, rest rotation grazing is another widely used system, especially on public lands. This approach involves deferment in some years, complete nonuse in some years and continuous grazing in other years. The kind of grazing applied is rotated among the various pastures to maintain a steady state stocking rate of the range over years. A variety of grazing systems that involve more than one herd of cows, controlled use and rotation over time have been developed. These often allow increased stocking rates but, along with that, more attention must be paid to management. The Merrill and high intensity low frequency systems typify this approach. Since the climate in range areas is highly variable, grazing systems have been developed to take advantage of variable moisture across the range area as in the best pasture approach where cattle are moved to the pasture where forage conditions are the best. Extremely intensive grazing managment is now becoming popular, such as short duration grazing where high stock densities are maintained for short periods of time with a rapid rotation through the various pastures. The Savory grazing method now called holistic resource management has become well known in recent years. This approach includes a complete analysis of ranching operations and economics to define where investments should be made followed by development of a grazing program that usually is similar to short duration grazing. A problem with these grazing systems, all of which can be appropriate, is that they are often implemented and followed rigidly with little flexibility exercised with respect to changing conditions. The approach to grazing that will optimize livestock production and sustain the forage base is probably best termed prescription grazing. This simply means matching the cattle to the forage supply in a way that takes advantage of the forage base and is responsive to the variations in weather, needs of the forage to maintain its vigor and the varying nutritional demands of the livestock.

On the extensive rangeland base of the West using a variety of grazing systems, rangelands produce about 200 million AUM's of grazing per year, in their largely deteriorated state (table 5). The USDA suggested in 1974 that this could be nearly tripled economically and that biological potential of rangelands and current technology would allow an increase of about eight-fold.

TABLE 5.   POTENTIAL GRAZING FROM U.S. RANGE AND LAND INVESTMENT COST PER AUM PER YEAR

AUM's in millions	Cost
200	3.04
300	3.22
360	3.34
400	3.42
560	3.72
1700	Not estimated

Source: USDA-Opportunities to Increase Red Meat Production from Ranges of the United States.

Increasing Cattle Production.   Increased use of rangelands for cattle production can improve economic efficiency by substantially decreasing the cost of maintaining the brood cow herd as well as replacing part of the forage requirement of growing stock.   This is obviously easier in some places than others and perhaps most difficult in the Northern Great Plains.   A return to more extensive exploitation of rangelands for livestock production must be done with a greater environmental cautiousness than historically, if it is to be sustainable.   As ranchers become more dependent on rangeland for forage, the complexities of this type of production system must be better understood.   Both the cow and the range forages are biological entities. Consequently, both are changing daily and the balance between exploitation and preservation must be attained to maintain a viable system.   If this is to be accomplished, the rancher can expect increased profit from his business.

A grazing program in the High Desert of Oregon illustrates this concept to some extent.   The sagebrush (Artemisia tridentata)-grass rangeland of the High Desert are typically grazed from May to October under deferred or rest rotation at six to ten acres per animal unit month, usually with about 10% of the range seeded to crested wheatgrass (Agropyron desertorum).   That same range under more intensive "prescription" rotation has been successfuly grazed (for 14 years) at three to four acres per animal unit month from March through December.   What changes from the more extensive practices of the past were made?   Careful attention is paid to the production requirements of class of stock and good feed is not wasted by exceeding nutrient requirements of the herd by feeding "luxury" levels of nutrients.   Primary attention is paid to the steer herd that is rotated in front of the cow herd.   Grazing is timed to direct growth of forage so that regrowth, which cures well for fall feed, is available for the cow herd in the fall rather than mature, nutritionally-deficient grass. Pasture sizes were decreased to about one or two thousand acres to improve distribution.   Water was likewise

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developed to improve livestock distribution. Sagebrush is controlled in appropriate areas to increase forage growth. The key to success of this program is the attention paid to improvements made in forage quality and palatability.

With further intensification of management, greater gains in efficiency are possible. Utilization of seeded pastures is good but recent research suggests the 80% utilization we see may really be only about 30% of the forage crop because of leaf senescence and loss. When a plant is grazed, it takes about 10 days in this environment for the regrowth to be available for regrazing. If the cattle were rotated weekly, we could increase utilization, forage production and quality of forage simultaneously. With intensive management, we should be able to maintain current levels of animal productivity with a grazing intensity of two or less acres per animal unit month. To fully understand the impacts of this more intensive utilization of the High Desert range, nutrition and behavioral responses of cattle will become more important and new information about animal behavior, mineral nutrition, intake and animal health will assist in fine tuning the grazing program. When grazing management finally reaches this level of intensity, we will allow the genetic potential of the cattle to be more fully realized and open opportunities to develop cattle breeds for improved adaptation to this kind of production system.

Constraints to Livestock Production. Livestock production and utilization of rangelands are controlled by many independent and interacting factors. Laws and policies of federal, state and local governments affect what can really be done on rangeland. Federal land use is carefully controlled or forbidden by wilderness laws, endangered species laws, multiple-use laws, and many others. The federal policies to enforce the laws limits to some extent the nature of livestock grazing programs. State laws and county ordinances restrict private land use. Economics is a driving force on most ranches. Concerns for competing uses for investments, costs of operations, profitability and rules from the banker all influence grazing management decisions. Natural forces constrain the biological potential of grazing livestock. Distribution of animals on range is influenced by availability of water and topography. Weather patterns influence annual forage yield, quality, species composition and availability. The mosaic of range types on the ranch is usually not at an optimum balance for production.

Tradition and habits of ranchers is a major determinant of action. In general, ranchers are satisfied with the way they currently do business and will generally operate with a low risk philosophy.

Two factors are especially important to range scientists who are working to improve livestock production systems on rangeland. Knowledge and understanding of a multitude of factors is limited. Range as a disciplinary area began in the 1950's, largely as a refinement from plant ecology. Consequently, only a few years of intensive research have passed. We need much more information about livestock production potentials and requirements on rangelands. Do we have "perfect" cows? How many perfect cows should breeders develop to fit the diverse rangeland systems in the West? Though much of the range research emphasis of the past has been on forage, we need considerably more information about forage potentials and requirements.

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Should we emphasize native or domestic forages? There is considerable interest in biotechnology now but, in reality, there has been little basic plant breeding work done on range plants. Range researchers are not even worried about a super plant. A few good ones would be a great step forward. The diversity of researchers that work with range livestock is also a problem. We sometimes don't talk to each other and when we do we have such diverse perspectives we probably don't really understand each other. All of us in science should bear this in mind when communicating across disciplines.

One of the greatest constraints to livestock production is individual creativity. We need to apply knowledge in more profitable ways. We are working with complex ecological systems and have clearly not attained full, sustained value from the rangelands in these production systems.

Potentials to Improve Productivity. Improved management or better knowledge will help increase efficiency and productivity of range livestock in almost every facet of the production system. Grazing mangement could easily be utilized to double current stocking levels in the sagebrush/grasslands of Oregon and increases in stocking on our forested ranges could increase eightfold with improved mangement. Increased use of rangelands would decrease dependency on fed forages to reduce costs of operation. Revegetation of the depleted brushlands can bring about substantial increases in productivity. On sagebrush/grass ranges of the Intermountain West, revegetation has brought stocking increases from 20 acres per animal unit month to one or two acres per animal unit month. Water developments are all that are needed to make millions of acres in the West grazeable. Limited livestock water is probably still the greatest constraint on range use in much of the West. Gains in forage productivity through biotechnology could be impressive by developing more adapted forages. Fertility and water management in the soil has potential to increase forages at low cost. Finally, weed control could be more widely practiced to reclaim deteriorated land and, more importantly, to prevent loss of good rangelands to noxious weeds.

Research. Any breakthrough that increases profitability of livestock pro- duction on rangelands will probably come through research. WRCC-40, the Western Regional Committee of the agricultural experiment stations for range research, completed an analysis of research needs in range management in 1984 (table 6). Currently, much of the effort is in range improvement areas, though generally the research effort is well distributed among the various categories.

In the future, we will see considerable intensification of livestock grazing management on rangelands because the application of research findings is cost effective. We will see cattle and sheep in high demand by foresters as a means to control weeds in forest plantations because of the cost of her- bicides and extreme pressure by politically active groups to eliminate pesticide use. This could bring about a major change in some livestock pro- duction systems of the far West.

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TABLE 6. PERCENT OF CURRENT RANGE RESEARCH, EXCLUDING ARS, IN THE ELEVEN
WESTERN STATES AND NEEDED LEVEL OF INCREASED EFFORT

Research area	Percent current emphasis	Needed magnitude of increased effort
Inventory and classification	7	2[1]
Range improvement	22	2
Grazing systems	13	3
Ecological impacts of management	11	2
Livestock (nutrition)[2]	14	2
Basic (physiology of plants)[2]	19	2.5

[1] Increase over current level, 2 = double effort.
[2] Primary focus needed.

However, with all the intensive management systems that surely will develop, the majority of the rangelands will continue to be managed extensively. The majority of cattle producers will need cattle that can range over rough topography, withstand extremes of temperature, maintain reproduction and yield under marginal nutrition and require little regular observation. The innovators may show the way to utilize more productive cattle in the range environment by managing ranges to provide better production conditions.

Can cattle breeders develop breeds or lines of range cattle that are more "user friendly"?

Literature Cited

Bedell, T. E. And T. Stringham. 1984. Forage sources for eastern Oregon cattle ranches with federal grazing permits. 1984 Progress Report. Research in Rangeland Management. Oregon State Univ. Agr. Exp. Sta. Spec. Rep. 715, pp 7-15.

Forest-Range Task Force. 1972. The nation's range resources - a forest-range environmental study. USDA Forest Service. Forest Resource Report No. 19. 147 p.

USDA Inter-agency Work Group on Range Production. 1974. Opportunities to increase red meat production from ranges of the USA. Phase I--nonresearch. 100 p.

FORAGE-ANIMAL INTERACTIONS

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Summary

Grazing management on tame pastures focuses primarily on increasing forage harvest efficiency; however, on rangelands there is an additional objective of range improvement through management of secondary plant succession. The grazing animal is the component of the system that is managed directly through: (1) selection of kinds and classes; (2) selection of season of grazing; (3) setting the stocking rate; and (4) design of the grazing plan. The dietary preferences and nutrient requirements of the animals must be matched to the kinds and quality of vegetation available. Maximum animal production is obtained when forage is grazed before it has matured; however, to obtain range improvement, the desirable forage species must be allowed to reproduce. This creates a basic conflict between maximizing range improvement and animal production. The optimum stocking rate is not a constant from year to year but will lie between the points of maximum gains per animal and per hectare. As harvest efficiency is increased through the application of higher grazing pressure, the need for flexibility in stocking rate increases.

Grazing systems are designed to control selective grazing problems. Selective grazing is intensified under low grazing pressures and is reduced as grazing pressure increases to high levels. Deferred-rotation grazing systematically defers all pastures to allow desirable plant species to recover from heavy use. Intensive rotational grazing systems seek to alter selective grazing by controlling both the frequency and intensity of defoliation to achieve specific plant and animal production objectives.

Introduction

Grazing is practiced on most of the world's terrestrial ecosystems, including rangelands, forest lands, and croplands. Range and pasture lands provide most of the forage that supports the world's ruminant animals. These animals are the source of meat, milk, hides, fiber, by-products, and recreation in the form of hunting and viewing. They are a vital link in both the food chain and the economic structure of most countries. In many areas of the world, the sustained production of grazing animals from rangelands is threatened by the lack of proper understanding and management of the forage-animal interactions.

The objectives for grazing management can be grouped into three broad categories: economic, biological, and personal. Economic objectives may include maximizing net income, reducing income variation, reducing risk, improving cash flow, reducing capital required, and many others. Biological objectives could include increased calf crop and weaning weights, increased stocking rates, larger wildlife populations, improved range condition, reduced erosion, and others. Under personal, I would include those that result from preferences of the manager or owner who may "just want to do it this way".

It is very important for management to focus attention on the selection of objectives. It would be nice if there was a management system that would maximize all objectives. However, in the "real world", this is impossible. There will always be trade-offs that have to be made. For example, you cannot maximize production per individual animal and production per hectare at the same time, nor is it generally possible to maximize net income and reduce risk simultaneously. Thus, the selection of objectives requires making choices and setting priorities.

The objective of this paper is to present a summary of several critical interrelationships between plants and animals in grazed ecosystems and to present some principles which can serve as guidelines for the management of grazing.

<center>Soil-Plant-Climate-Animal</center>

The response of plants to grazing is conditioned by soil and climatic variables. Thus, a discussion of plant-animal interactions must logically begin with a discussion of soil-plant-climate interactions.

Climate. Climatic variables of major interest are precipitation, heat, and light. The amount of moisture available generally determines the potential forage production. The amount of heat determines the kinds of plants that are adapted and the seasons during which plant growth can occur. The duration and quality of light control physiological processes, such as flowering, in some plants. Light intensity is an important factor influencing photosynthesis and may play an important role in plant succession as plants of different stature and life-form compete. Of these variables, precipitation is the least predictable and exhibits the greatest variance from season to season and year to year. Thus, it is generally the climatic variable of greatest interest when evaluating forage-animal interactions.

Soil. There are many soil factors that affect plants; however, only a few are of major interest in evaluating forage-animal interactions. Forage production of any given soil is primarily a function of the availability of moisture and nutrients for plant growth. The amount of moisture available for plant growth is a function of many factors, which include: the amount of precipitation received, the amount that infiltrates into the soil, soil texture, soil depth, soil organic matter, and the amount of moisture that evaporates or percolates beyond the rooting depth of the plant. Soil depth and texture are the best indicators of the moisture-holding capacity of a soil.

Nutrient availability is influenced by the parent material from which the soil was derived, the degree of leaching which has occurred, and the cation exchange capacity. In arid and semiarid environments, nitrogen is generally the primary limiting nutrient. In more humid climates, leaching may have reduced phosphorus and potassium to levels that limit plant growth. Soil organic matter is extremely important in determining the cation exchange capacity of soil and, thus, the size of the nutrient pools. Grazing, through its effect on organic matter contributions to the soil from both roots and aboveground plant parts, may have a very significant impact on the nutrient status of soils.

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In arid and semiarid environments, water is generally the first limiting factor for forage production. In humid environments, nitrogen generally is the first limiting factor. Thus, on most rangelands, fertilization is seldom if ever practiced; whereas, on tame pastures in humid climates, fertilizers are routinely applied. Because of reduced moisture availability, plant growth may occur during only brief periods on many rangelands. Under higher rainfall, forage production may extend across most of the year when heat is not limiting. Rangelands are frequently grazed yearlong, thus requiring that animals be sustained on dormant range. Most grazing on tame pastures occurs during periods of active growth with little use of dormant forages. It is important to understand these relations when evaluating forage-animal interactions.

Plant. The plants on rangelands have been subjected to natural selection. Those which are best able to survive and reproduce under existing natural conditions occupy the site. Plants on tame pastures are selected for various characteristics, usually including high levels of productivity, and may have limited ability to survive and compete under natural conditions. Cultural inputs such as fertilization, weed control and tillage are used to maintain the productivity of tame pastures; whereas, they are used only infrequently on rangelands. This difference in the management of ranges and tame pastures is very important when evaluating the intensity of grazing that may be applied. The low potential productivity of many ranges precludes the profitable application of expensive cultural inputs to maintain forage production at levels near site potential. The increased cost of energy relative to the price received for livestock is making it increasingly difficult to justify intensive inputs on many tame pastures. There is a great need to develop management schemes that reduce dependence on the infusion of energy inputs to maintain the productivity of the systems. Many intensive forage-livestock production schemes are based primarily on the energy-rich cultural inputs. Unless a new, abundant, cheap source of energy is developed, these production systems will continue to become less profitable.

Vegetation on rangelands is comprised of a great diversity of species with broad genetic variation within most species. This diversity is an asset to both the stability of the plant communities and to the animal as it selects its diet. The diversity in plant species adds stability to the nutrient intake of the grazing animals by allowing them to shift their diets from species to species as seasons change and as the degree of utilization increases. The nutrient intake of animals grazing on monocultures follows the seasonal trend for that species.

Animal. Some parallels may be drawn between the plants and animals. There are both native and introduced animals. On tame pastures, both the animals and the plants are introduced and managed directly. Although rangeland vegetation consists almost entirely of native plants, the primary grazers on most ranges are introduced livestock.

In grazing management, the animal is the component of the system that is managed directly. Factors that are subject to direct action include the following:

-- Selection of the kinds and classes of animals

-- Selection of the seasons of grazing

-- Setting the stocking rate

-- Design of the grazing plan

The responses of the vegetation and animals to management decisions are not under direct control of management. This may be frustrating to some persons who like to see a direct response to their actions. For example, they plant a grass and see it grow or they apply a herbicide and see brush die. In grazing management, you may change the number of animals, thus changing the forage:animal ratio; this, in turn, will change diet selection of the animals; this may change nutrient intake and animal production; meanwhile, the change in grazing pressure will result in a shift in the competitive relationships among plant species causing a change in the plant community; this, in turn, may result in further changes in diet selection and animal production.

Because of the complicated nature of the relationships and the indirect nature of both plant and animal responses to grazing management, it is essential to understand the principles that govern the system. Some of the principles which form the basis for making grazing management decisions will be described and discussed.

The two most basic biological goals for grazing management generally are: (1) to maintain or improve the productive potential of the vegetation, and (2) to increase animal production. The second objective could apply to either domestic or wild animals. Each of the management factors listed above that are subject to direct action will be discussed with respect to achieving specific objectives.

Management Principles

Kind and Class of Animal. This is generally a long-term decision. However, it is a very important one. Several factors that should be considered in making the decision are: (1) the kinds and amounts of vegetation available and its quality, (2) the topography, (3) predators, (4) poisonous plants, (5) availability of animals, (6) availability of markets for different kinds and classes of animals, (7) diseases, and (8) management skills and preferences.

Matching the dietary preferences and the nutrient requirements of the animals to the kinds and quality of the vegetation available is the first important step. We generally find cattle utilize large amounts of grasses, sheep prefer forbs, and goats utilize browse effectively. Certainly, all three kinds of animals utilize all three forage classes, but these diet preferences have been well documented. Ranges that support combinations of the different forage classes are more efficiently utilized by a combination of animals. The most efficient combination of animals depends upon the availability of the different kinds of forage. The principle involved is to match

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the animal's dietary preferences, nutrient requirements, and foraging abilities to the kinds, amounts, and quality of the forage resource. This improves the efficiency of both forage utilization and animal production.

The nutrient requirements of animals vary considerably among kinds and classes. (NOTE: Nutrient requirement is used in this paper in the context of nutrient density or percentage concentration in the diet.) Nutrient requirements tend to be inversely proportional to the size of the animal; smaller animals having the higher nutrient requirements. Nutrient requirements are higher for lactating than for dry animals and for growing than for mature animals. Pregnancy also increases nutrient requirements slightly.

It is generally not good economics to graze animals having high nutrient requirements on forage with low nutrient content. Either the feed bill will be high or the level of animal performance will be low! Selecting cows with high milk-producing potential may be good management if high quality pasture is available but will not be advisable on range that supports mainly warm-season perennial grasses and has a long dormant period. Neither is it wise in an economic sense to utilize high quality forage with animals having low nutrient requirements.

Season of Grazing. Forage quality varies seasonally and between plant species and forage classes. Forages produced during the cool season are of higher quality than those produced during the warm season. Forage quality declines rapidly with advancing plant maturity; and dormant forage is poor feed, especially when it has been leached by rain or dew. Leaf is higher quality than stem and does not decline in quality as rapidly.

Most rangelands in the Southwest are grazed yearlong. Few tame pastures or mountain ranges in the western U.S. are grazed yearlong. Seasonal use of ranges in Texas generally results when they are grazed in combination with tame pasture or forage crops or when they are grazed with stocker animals that are bought and sold annually. Dormant-season grazing with rest during the growing season is used to obtain range improvement. Tame pastures are grazed primarily during their period of active forage growth.

There are two important principles which should be considered when making decisions regarding season of grazing. First, animal production is greatest when forage is grazed soon after it is produced and before it has matured. Second, to obtain range improvement, the desirable forage species must be allowed to reproduce. Thus, when range improvement is an important goal, there will generally need to be some reduction in animal production to achieve the improvement. It is obvious that, on tame pastures and good condition rangelands where range improvement is not an objective, the grazing plan can be designed to maximize animal production. This is why tame pastures should be fully utilized during the growing season. There is no logical reason to defer use of most tame pastures during the growing season and utilize them during the dormant season. These expensive forages should be grazed to harvest the maximum amount of nutrients for high levels of animal production.

Rangelands generally provide the flexibility in forage systems where they are combined with tame pastures. This means that the tame pastures are

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grazed when they provide the most nutrients and the rangelands are used to fill the gaps. This not only utilizes the most expensive forage most efficiently, it also can promote range improvement by providing growing season deferment for rangelands. However, it is important that the relative carrying capacity of the range and tame pasture be properly balanced to prevent overutilization of the range.

Range sites may differ significantly in their suitability for grazing during different seasons. Cool-season herbaceous forage and evergreen browse will generally provide better grazing during the winter and early spring; whereas, warm-season forages are best suited to use during late spring, summer or fall. Large pastures with a mix of sites allow animals to rotate their grazing seasonally. Smaller pastures, which contain less variation in vegetation, may require the use of seasonal adjustments in grazing to match the forage.

Stocking Rate. Stocking rate is the most important grazing management decision. Understocking results in wasted forage and lower total animal production. Overstocking results in damage to the forage resource and reduced animal production. Moreover, the optimum stocking rate is not a constant but varies depending upon the current year's conditions. Since we do not have accurate weather predictions, one might say that we are shooting at a target that moves randomly up and down through time. Thus, if we aim high and the target moves down, the result is overstocking. However, if we aim low and the target moves up, the result is understocking. Clearly, principles are needed to guide stocking rate decisions.

Strong relationships exist between stocking rate and both range improvement and animal production. An understanding of these relationships is essential to the design of grazing management plans.

Stocking rate is a function of three things: (1) the land area, (2) the number of animals, and (3) the time that the animals graze on the land. Since adding numbers of cows, calves, sheep and goats has no meaning, the animal unit (AU) has been defined as a standard forage-demand rate of 12 kg per day. Total forage demand by the animals is a product of the demand rate and time of grazing (AU X Days = AUD). Thus, stocking rate represents the total forage demand (AUD) applied to a given area of land during a specified time period and is expressed as AUD, AUM or AUY/hectare. However, the relationship that is most important is that between forage demand and forage available, which is called "grazing pressure". Grazing pressure is expressed as AUD/kg of forage available and can be related directly to stocking rate by determining forage production (kg/ha).

Harvest efficiency is expressed as the proportion of the total forage produced that is actually consumed by the grazing animals. Increasing the grazing pressure increases harvest efficiency. However, increased harvest efficiency is only good up to a certain point. Where that point is depends upon the kind and condition of the vegetation and the management objectives. Maximum harvest efficiencies are achieved from very intensive rotations stocked at high grazing pressures; however, high grazing pressures may reduce nutrient intake of the animals, thus reducing animal production.

High grazing pressures also result in close defoliation of preferred plants. The ability of plants to tolerate intensive defoliation depends primarily upon the genetics of the plant species and the presence of moisture and fertility to support plant growth. Plants under favorable growing conditions have the opportunity to recover from close grazing. The response of a plant to severe defoliation is a function of its ability to produce new leaves and shoots and its ability to allocate carbon and plant nutrients to promote this growth. Those species that have many meristems and buds that are not accessible to grazing and that can activate them quickly will be resistant to grazing.

The correct stocking rate for a particular pasture will depend upon the desired level of animal performance, the ability of the vegetation to withstand grazing and the range improvement goals. Grasses such as bermudagrass, bahiagrass, K. R. bluestem, buffalograss, common curlymesquite, crested wheatgrass and Russian wildrye are well suited for intensive grazing. Many taller grasses and bunchgrasses are not well suited to withstand intensive grazing. Therefore, intensive grazing (high grazing pressure index) will shift the species composition of the vegetation towards short grasses; whereas, lower grazing intensities will allow the taller species a competitive advantage. Tall grasses and bunchgrasses generally are more productive than short grasses, and they root deeper, making them more drought tolerant. When growing in mixed stands, tall grasses usually will be grazed more intensively than short grasses. If grazed too intensively or frequently, they will decline.

The law of diminishing returns governs the relationship between stocking rate and animal production. Forage may be considered as the basic resource and animals as the inputs. At low stocking rates, the production per animal is not affected by the addition of an additional animal. As the stocking rate is increased, the forage resource remains constant or begins to decline, and a point is reached where animals are competing with each other for food. The addition of another animal will reduce the production of each individual animal on the pasture, but the total animal production from the pasture will continue to increase. If enough animals are added to the pasture, individual animal production will decline to the point that total production will also decline. If you are stocked to this level, you are probably losing both money and your forage resource. Proper stocking will be greater than the point of maximum gains per animal and less than the point of maximum gains per unit of land.

One final point we will consider about stocking rate is the dilemma of economic returns to land and risk. Land is the largest single cost of production in most range livestock operations, and the net return to land is generally low. Increasing animal production per unit of land is an obvious method for improving total returns. Since proper stocking rates are below the point of maximum animal production per unit of land, there appears to be an opportunity for increasing returns. If grazing can be controlled to prevent damage to the vegetation, higher stocking rates can be used to increase harvest efficiency. However, be aware that as the harvest efficiency increases, the cushion of "reserve forage" decreases. This means that more frequent adjustments to stocking rate will be required to prevent

overstocking in poor years. Let me emphasize, the higher the harvest effi-
ciency, the greater the requirement for flexibility in stocking rate and the
greater the risk!

Designing the Grazing Plan (Grazing Systems). Basically, grazing systems
are plans for the rotation of livestock among two or more pastures. They
should be the final, not the initial, point of planning for grazing. The
grazing system is set in the context of the choices of kinds and classes of
animal, season of use, and stocking rate. While the choice of grazing
system may influence these previous decisions, it should not be the first
decision in the planning process.

The first questions to consider are: "Why rotate animals? Why not graze
pastures continuously?" The answer is that animals are rotated to control
selective grazing problems. If you have no selective grazing problems, then
you probably will not benefit from rotational grazing. However, this is an
unlikely situation on most rangelands.

Grazing distribution under continuous grazing can be controlled best on
intensively managed tame pastures consisting of one or two species that are
highly resistant to grazing. High grazing intensitites result in uniform
utilization of forage soon after it is produced. Mature forage does not
accumulate, and growth rapidly replaces the forage that is consumed.
Grazing is restricted to the growing season so there is no need to conserve
standing forage for dormant-season grazing.

The situation described above is not typical of most rangelands. Rangeland
vegetation consists of complex mixtures of plant species that vary greatly
in palatability and resistance to grazing. The species have different
environmental requirements for growth, and develop and mature at different
times. Grazing pressures are generally moderate to low (NOTE: Grazing
distribution is seldom a problem on overstocked ranges!) Opportunities for
plant growth on arid and semiarid ranges are frequently limited to one or
two relatively short periods during the year, and regrowth following inten-
sive defoliation may be delayed or prevented by lack of moisture. It is
usually necessary to conserve standing forage for grazing during dormant
periods. Under these conditions, selective grazing and grazing distribution
problems are the rule not the exception!

There are almost an infinite number of schemes for rotating livestock, based
on various numbers of pastures and herds and on different lengths of grazing
and rest periods. In order to try and make some sense of the many alter-
natives, I will describe two basic types of rotation grazing systems and
then outline some basic principles associated with them.

Deferred-rotation grazing has no more than two pastures per herd of
livestock, and the length of grazing periods equals or exceeds resting
periods. Stocking densities (AU/ha) are not increased greatly, and animals
are not moved frequently. The objective is to systematically defer grazing
on all pastures to allow desirable plant species to recover from heavy use
and reproduce. Individual animal performance is generally good at moderate
stocking rates; however, deferred-rotation systems do not give good

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vegetation or animal response at high stocking rates. Deferred-rotation grazing systems are a good choice if management objectives include steady range improvement, high levels of individual animal performance, minimum risk and miminum short-term decision making.

Intensive grazing systems may be the choice of the manager who wants to try for more rapid improvement or for greater production per unit of land area. Intensive systems utilize three or more pastures per herd. They generally require more capital investment, more frequent decisions, and more frequent movement of livestock. The more pastures per herd in the grazing system, the more intensive the management required. As is usually the case, greater potential for gain carries with it greater risk for loss.

Operation of intensive grazing systems requires frequent decisions, such as how long to graze each pasture and the sequence in which pastures are grazed. These decisions, combined with the stocking rate, determine the frequency and intensity of grazing and have a large effect on animal production. Intensity of grazing has already been discussed under the topic of stocking rate. However, under grazing systems, the grazing intensity can be increased by concentrating animals on less area or by extending the grazing periods. Long grazing periods, followed by long rests, are used in high-intensity, low-frequency (HILF) grazing systems. This results in good range improvement but, unfortunately, high grazing pressure and the large amounts of mature forage that accumulate during rest periods usually reduce nutrient intake and animal production. However, if intensity of grazing is reduced to a moderate stocking rate, acceptable levels of animal production may be obtained while making rapid range improvement.

An understanding of the general responses of plants and animals to different intensities and frequencies of grazing will help to predict the effects of rotational grazing systems. Individual animal production will increase as the frequency of grazing increases and, as the intensity decreases, within the limits of stocking rates that are usually employed. Gain per hectare increases as frequency and intensity of defoliation increase, until the overall degree of forage utilization is high. Range improvement will increase as frequency and intensity of grazing decrease. If the manager wishes to strike a balance among these three management objectives, the obvious choice will be intermediate levels of frequency and intensity of grazing. Each management unit will have a different combination of resources and objectives; thus, the choice of grazing strategy will vary.

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GRAZING BEHAVIOR OF CATTLE IN A RANGE ENVIRONMENT

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Grazing activities and travel of range livestock are reviewed. Recent research at this Laboratory with activities of range cattle under harsh winter weather conditions is presented and some considerations for developing range management strategies and selection criteria for range cattle are discussed.

The Range Environment

Rangelands can be regarded as all land producing native forage for animal consumption, including lands that are revegetated naturally or artificially to provide a forage cover that is managed like native range (ASRM, 1964). About one-half of the earth's land surface is rangeland (Stoddart et al., 1975). In the 17 western states, it is estimated that there are 380.8 million hectares of rangeland (USDA, 1981). This rangeland is the primary source of forage for many free-ranging domestic animals and wildlife. Rangeland is often characterized by unproductive soils, erratic low precipitation, rough topography and temperature extremes (Stoddart et al., 1975).

Forage produced on rangeland can be highly variable in quantity (Holscher and Woolfolk, 1953; Wight et al., 1983) and quality (Cogswell and Kamstra, 1976). Animal performance can also vary greatly from year to year (Black et al., 1938). The importance of diet quality and level of intake on performance of cattle are well documented (NRC, 1984). Other factors also play important roles in determining the performance of range livestock. Osuji (1974) reported that the maintenance requirements of foraging livestock may be 25 to 50% higher than those in confinement. Extreme weather conditions increase maintenance requirements and decrease forage utilization (NRC, 1981). Supplemental feeds can affect forage digestibility, forage intake, (Kartchner, 1981; Rittenhouse et al., 1970) and animal performance (Black et al., 1938; Parker et al., 1974). Livestock management practices such as type of supplement (Kartchner, 1981; Cochran et al., 1984), interval between supplementation (Kartchner and Adams, 1982), and time of supplementation may also affect performance (Adams and Kartchner, 1983). Range management practices also influence animal performance. In Montana, Houston and Urick (1972) reported that paddocks seeded with crested wheatgrass (Agropyron desertorum) or Russian wildrye (Elymus junceus) provided green forage 10 days to 5 weeks earlier in the spring than native range and that cow-calf performance was greater on seeded paddocks than on native range. Other research has shown that cow-calf performance decreased as stocking rate increased on native range, although the greatest animal production per hectare was achieved at moderate stocking rates (Houston and Woodward, 1966).

Variable conditions, such as between and within vegetation types and range sites, create unique situations for selection of range cattle and their management. Because of this variation, it is unlikely that there is an ideal type of cattle or uniform management criteria for all rangelands.

Several researchers (Culley, 1938; Peterson and Woolfolk, 1955; Sneva, 1970; Adams and Kartchner, 1983) have discussed the value of animal behavior principles in developing range and livestock management strategies. Some behavior principles may also contribute to selection criteria for range cattle.

Grazing Behavior

Grazing patterns of range cattle have been studied over a broad range of conditions (Cory, 1927; Peterson and Woolfolk, 1955; Lampkin et al., 1958; Dwyer, 1961; Wilson, 1961; Wagnon, 1963). These studies generally show two major or primary grazing periods each day for range cattle, one beginning about sunrise for 3 to 6 hours and a second beginning in the late afternoon or early evening of similar duration. Additional intermittent or secondary grazing periods occur at other times of the day and night. Although range cattle have been observed grazing at all hours of the day and night (Wagnon, 1963; Kropp et al., 1973), timing of the secondary grazing periods is influenced by grazing pressure and climatic factors (Arnold and Dudzinski, 1978). Dwyer (1961) observed cows grazing Oklahoma range during the summer and reported that total grazing time decreased as air temperatures increased from 26.5 C. In a winter study, Utah researchers (Malechek and Smith, 1976) found that range cows spent less time grazing on colder than warmer days. In another winter study, Canadian researchers (Smoliak and Peters, 1955) also found that grazing increased with increasing temperature. Arnold and Dudzinski (1978) summarized a number of behavior studies and reported a range in daily grazing time from about 5 to 15 hours per day in beef cattle, with the greater percentage of observations occurring between 7 and 11 hours per day.

Intake by grazing animals is a function of time spent grazing and rate of intake. Rate of intake is variable as is grazing time. Allden (1962) reported that the rate of forage intake of sheep increased as forage availability increased, but that time spent grazing decreased. Other research by Arnold (1975) has shown greater forage intake for ewes in late pregnancy than for dry, nonpregnant ewes; however, these differences were more readily explained by a higher rate of consumption than by time spent grazing. Time of supplementation may also affect rate of intake. Adams and Kartchner (1983) observed that foraging steers supplemented with corn grain in the morning consumed an average of .9 kg of forage for each hour of grazing time while steers supplemented in the afternoon with the same amount of corn consumed an average of 1.1 kg of forage per hour spent grazing.

Nutrient intake in grazing animals is a function of time spent grazing, rate of consumption, and diet quality. Leigh and Mulham (1966) found that at certain times of the yea high proportions of the diet were selected from plants comprising very small portions of the available forage. This indicated a high degree of selectivity by animals for individual plants. Other research shows high grazing selectivity for individual portions of plants (Cook and Harris, 1950).

Forage utilization on rangeland is dependent on animal selectivity, animal distribution and stocking intensity. Distribution of cattle is affected by factors relating to animal behavior. Mueggler (1965) found that the

steepness of slope of rangeland and water distribution had a significant influence on the distribution of cattle. Researchers in Oregon (Roath and Krueger, 1982) found vegetation type, slope, and water distribution important variables in determining utilization by beef cattle on forested range. Other research by Dwyer (1961) suggests a relationship between grazing location and wind direction.

Although several studies have compared grazing behavior of different animal species (Arnold and Dudzinski, 1978), few have compared grazing behavior of different breeds of cattle. New Mexico researchers (Herbel and Nelson, 1966) compared the grazing activities of Hereford and Santa Gertrudis cattle grazing a semi-desert range. They found that Hereford cows spent significantly more time grazing than Santa Gertrudis cows on a yearlong basis but variation in grazing time occurred within season of the year. Kropp et al. (1973) observed Hereford, Hereford x Holstein and Holstein heifers grazing a tall grass range and found that differences in time spent grazing were small between breeds.

Travel of Range Cattle

The distance traveled contributes to the maintenance requirement of grazing cattle (Osuji, 1974) and may be an important variable in developing management strategies for rangelands and range livestock. In range cattle, daily travel is highly related to the grazing activity (Wagnon, 1963), but other factors affect travel. Shephard (1921) observed steers grazing in paddocks of different sizes and reported that the larger the paddock, the greater the distance traveled. Texas researchers (Anderson and Kothmann, 1980) found that heifers under a continuous grazing system traveled an average of 5.2 km/day, while those grazing under a high-intensity, low-frequency system traveled an average of 3.6 km/day. Under both systems, distance traveled was highly correlated with crude protein, digestible energy and ratio of leaf blade to stem of the diet. Wagnon (1963) found that cows in a lightly grazed paddock traveled further each day than cows in a closely grazed paddock. Winter supplementation studies in Texas (Box et al., 1965) and California (Wagnon, 1963) showed that nonsupplemented cows walked a greater distance each day than did supplemented cows. In contrast, Adams and Kartchner (1983) observed that foraging yearling steers receiving corn supplement traveled a greater distance than did nonsupplemented steers. Herbel and Nelson (1966) compared the daily travel of Hereford and Santa Gertrudis cattle on a semidesert range in New Mexico and found that Santa Gertrudis cows traveled 12.5 km/day compared to 7.9 km/day for Hereford cows. Other factors such as availability of water, rainfall, air temperature and estrus will also affect travel of grazing cattle (Dwyer, 1961; Anderson and Kothmann, 1980).

Grazing and Travel of Range Cattle Under Harsh Conditions

Variables have been discussed which affect grazing behavior and travel of range livestock. Although the studies reviewed cover a broad range of environmental conditions, winter weather conditions in the Northern Great Plains are often much more severe than those reported in most studies. At Miles City, Montana, a low temperature of -54 C was recorded on January 13, 1888 and it is not uncommon for extended periods of cold temperatures (up to

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30 days) where the minimum daily temperature remains below –18 C. It is well documented that these periods of harsh weather conditions can result in loss of body weight and condition of range cows (Black et al., 1938; Kartchner, 1981). Loss of body weight and condition during harsh winter conditions can be explained in part by higher maintenance requirements associated with cold (NRC, 1984) and reduced forage digestibility (Christopherson, 1976; Kartchner, 1981). Behavior of range cattle during extended periods of harsh winter weather is not well documented, but Malechek and Smith (1976) showed that changes in grazing behavior occurred as air temperatures became colder. Two trials were conducted here at Miles City to evaluate effects of harsh winter weather on the grazing behavior of range cattle.

In the first trial, 12 crossbred cows were utilized. All cows were fitted with 8-day vibration recorders (Stobbs, 1970) in order to monitor animal grazing time. Grazing time was recorded continuously from December 9, 1981 to January 14, 1982. Cows grazed freely on a 300-hectare, broken-upland range site. Air temperatures during the study ranged from a high of 7.8 C to a low of –33.9 C. Average daily wind velocity ranged from 5.6 to 28.0 km/hour. Minimum and maximum time spent grazing in a day for individual cows was .5 and 11.6 hours, respectively. The relationship between independent variables of minimum daily air temperature and average wind velocity and the dependent variable of daily grazing time indicated a highly significant linear component using multiple regression procedures with air temperature accounting for a much larger portion of the sums of squares due to regression than did average wind velocity. The multiple regression equation was:

$$y = 9.26 + .123x_1 - .044x_2$$

where y = predicted total grazing time, hour/day
x_1 = minimum daily air temperature, C
x_2 = average daily wind velocity, km/hour

The times spent grazing predicted by this equation are presented in table 1 for selected air temperatures and wind velocities.

In trial 2, 12 Hereford cows were utilized; cows grazed on a 73-hectare, broken-upland range site. Eight of these cows were fitted with 8-day vibration recorders as previously described, and each of the 12 were fitted with a pedometer on the left foreleg in order to measure distance traveled as described by Anderson and Kothmann (1977). Grazing time and distance traveled were monitored continuously from November 22 through December 29, 1983. During this time period, air temperatures ranged from 12.3 to –39 C. Wind velocity data were not utilized in this study. The regression of daily grazing on minimum daily temperature indicated a significant (P<.01) linear component. The simple regression was:

$$y = 9.20 + .102x$$

where y = predicted total grazing
x = minimum daily air temperature

Grazing times at various air temperatures are presented in table 1. These studies both demonstrate that colder air temperatures between 0 to –40 C

TABLE 1. DAILY GRAZING TIME OF COWS AT VARIOUS AIR TEMPERATURES AND WIND
VELOCITIES[a]

Average daily wind velocity (km/h)	Minimum daily air temperature (C)				
	0	-10	-20	-30	-40
	----------------Grazing time (h/d)---------------				
	Trial 1				
0	9.3	8.0	6.8	5.6	
15	8.6	7.4	6.1	4.9	
30	5.6	5.1	4.7	4.3	
	Trial 2				
0	9.2	8.2	7.2	6.1	5.1

[a] Regression equations for trials 1 and 2 are given in the text.

result in significantly less grazing time by range cattle. Research by
Kartchner (1981) here at Miles City showed that under moderate winter con-
ditions range cows consumed about 1.8 kg of forage per 100 kg of body
weight. If a linear reduction in both intake and grazing time is associated
with decreasing air temperature, forage intake might be reduced to less than
.9 kg per 100 kg of body weight at air temperatures of -20 C or less. While
cattle seem able to increase forage intake rates to improve foraging effi-
ciency (Allden, 1962; Arnold, 1975), it is probable that such increases
would not be large enough to offset the reductions in grazing time. Intake
data for foraging livestock at various winter temperatures are not available
but a conclusion that a reduction in forage intake is associated with
decreasing air temperature is supported by the lower forage intakes and loss
of body weight of range cows reported for harsh weather conditions compared
to moderate conditions (Kartchner, 1981). In contrast to this theory for
grazing livestock, intake has been observed to increase in feedlot cattle at
colder air temperatures (Milligan and Christopherson, 1974). A reduction in
time spent grazing should result in a reduction of energy spent for main-
tenance (Osuji, 1974).

Means and standard deviations were determined for daily travel over 7-day
intervals. These values were then plotted for five different 7-day inter-
vals as a function of the average minimum daily temperature (figure 1).
These data show an inverse relationship between air temperature and distance
traveled when minimum air temperatures range between -8 and -30 C, with the
average daily travel increasing from 5.8 km/day at -9 C to 8.6 km/day at -30
C. Because much of a range cow's daily travel has previously been attri-
buted to grazing activity (Wagnon, 1963) and time spent grazing was lowest
at coldest temperatures, one might have expected a reduction in travel at
colder air temperatures. However, that response was not observed. The
increased level of travel at colder temperatures suggests that cattle may

have increased their locomotor activity to keep warm, as postulated for large animals by Hafez (1968). The travel data also show greater standard deviations at colder temperatures, suggesting that at extreme temperatures, genetic variation among cows may be more apparent.

FIGURE 1

DAILY TRAVEL OVER A WEEK LONG PERIOD OF
HEREFORD COWS GRAZING NATIVE FALL-WINTER RANGE
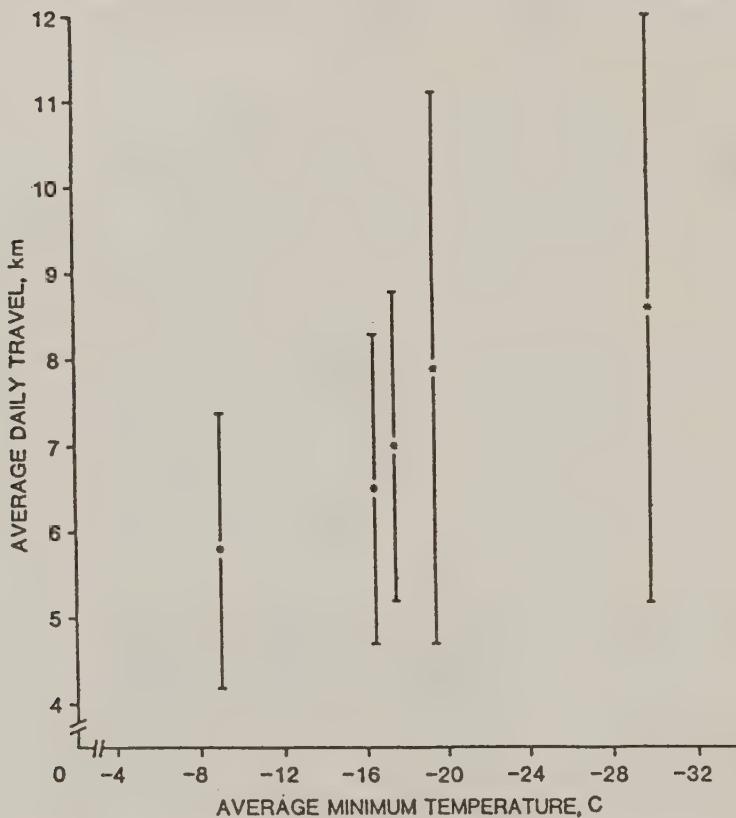
Grazing Behavior, Management Strategies and Animal Selection

Due to the broad variations in rangelands, management strategies and selection criteria for range cattle will vary according to vegetation type and range site. Management strategies can affect behavior of range livestock; therefore, management strategies should be identified to enhance distribution of cattle on the range, complement livestock and forage production and increase efficiency of production. Among the management variables that might be considered to complement animal behavior are cattle density, vegetation composition, forage quality, forage quantity, location of fencing, paddock size and shape, water location and distribution, weather, forced movement of cattle, and supplementation. Cattle should be evaluated and selected for traits which enhance distribution and acclimation to environmental conditions. While the body of literature is growing, more research needs to be conducted if principles of animal behavior are to be successfully integrated into range management strategies and range cattle selection

criteria. The potential appears great for using behavior principles to enhance our understanding of the grazing animal and to assist in increasing levels and efficiency of range and livestock production to meet an increasing food demand for a growing world population.

Literature Cited

Adams, D. C. and R. J. Kartchner. 1983. Effects of time of supplementation on daily gain, forage intake and behavior of yearling steers grazing fall range. Proc. West. Sec. Amer. Soc. Anim. Sci. 34:158.

Allden, W. G. 1962. Rate of herbage intake and grazing time in relation to herbage availability. Proc. Australian Soc. Anim. Prod. 4:163.

Anderson, D. M. and M. M. Kothmann. 1977. Monitoring animal travel with digital pedometers. J. Range Manage. 30:316.

Anderson, D. M. and M. M. Kothmann. 1980. Relationships of distance traveled with diet and weather for Hereford heifers. J. Range Manage. 33:217.

ASRM. 1964. A Glossary of Terms Used in Range Management. Amer. Soc. Range Manage., Portland, Oregon.

Arnold, G. W. 1975. Herbage intake and grazing behavior in ewes of four breeds at different physiological states. Australian J. Agr. Res. 26:1017.

Arnold, G. W. and M. L. Dudzinski. 1978. Ethology of free-ranging domestic animals. Elsevier Scientific Publishing Company, New York.

Black, W. H., J. R. Quesenberry and A. L. Baker. 1938. Wintering beef cows on the range with and without a supplement of cottonseed cake. USDA Bull. 603.

Box, T. W., G. Brown and J. Liles. 1965. Influence of winter supplemental feeding of cottonseed cake on activities of beef cows. J. Range Manage. 18:124.

Christopherson, R. S. 1976. Effects of prolonged cold and outdoor winter environment on apparent digestibility in sheep and cattle. Can J. Anim. Sci. 56:201.

Cochran, R. C., D. C. Adams, J. D. Wallace, M. L. Galyean and P. O. Currie. 1984. Cubed alfalfa hay or cottonseed meal-barley as protein supplements for beef cattle grazing fall-winter range. J. Anim. Sci. 59(Suppl. 1):281.

Cogswell, C. and L. D. Kamstra. 1976. The stage of maturity and its effect upon the chemical composition of four native range species. J. Range Manage. 29:460.

Cook, C. W. and L. E. Harris. 1950. The nutritive content of the grazing sheep's diet on summer and winter range in Utah. Utah Agr. Exp. Sta. Bull. 342.

Cory, V. L. 1927. Activities of livestock on the range. Texas Agr. Exp. Sta. Bull. 367.

Culley, M. J. 1938. Grazing habits of range cattle. J. Forestry 36:715.

Dwyer, D. D. 1961. Activities and grazing preferences of cows with calves in Northern Osage County, Oklahoma. Oklahoma Agr. Exp. Sta. Bull. B-588.

Hafez, E. S. E. 1968. Behavioral adaptation. In: E. S. E. Hafez (Ed.) Adaptation of Domestic Animals. Lea and Febiger, Baltimore, MD.

Herbel, C. H. and A. B. Nelson. 1966. Activities of Hereford and Santa Gertrudis cattle on a Southern New Mexico range. J. Range Manage. 19:173.

Holscher, C. E. and E. J. Woolfolk. 1953. Forage utilization by cattle on Northern Great Plains Ranges. USDA Circ. 918.

Houston, W. R. and J. J. Urick. 1972. Improved spring pastures, cow-calf production and stocking rate carryover in the Northern Great Plains. USDA Tech. Bull. 1451.

Houston, W. R. and R. R. Woodward. 1966. Effects of stocking rates on range vegetation and beef cattle production in the Northern Great Plains. USDA Tech. Bull. 1357.

Kartchner, R. J. 1981. Effects of protein and energy supplementation of cows grazing native winter range on intake and digestibility. J. Anim. Sci. 51:432.

Kartchner, R. J. and D. C. Adams. 1982. Effects of daily and alternate day feeding of grain supplements to cows grazing fall-winter range. Proc. West. Sec. Amer. Soc. Anim. Sci. 33:308.

Kropp, J. R., J. W. Holloway, D. F. Stephens, L. Knori, R. D. Morrison and R. Totusek. 1973. Range behavior of Hereford, Hereford x Holstein and Holstein non-lactating heifers. J. Anim. Sci. 36:797.

Lampkin, G. H., J. Quarterman and M. Kinder. 1958. Observations on the grazing habits of grade and Zebu steers in high altitude temperate climate. J. Agr. Sci. 50:211.

Leigh, J. H. and W. E. Mulham. 1966. Selection of diet by sheep grazing semi-arid pastures on the Riverine Plain. I. A bladder saltbush (Atriplex vesicaria)-cotton bush (kochia aphylla) community. Australian J. Exp. Anim. Husb. 6:460.

Malechek, J. C. and B. M. Smith. 1976. Behavior of range cows in response to winter weather. J. Range Manage. 29:9.

Milligan, J. D. and G. Christopherson. 1974. Effects of severe winter conditions on performance of feedlot steers. Can. J. Anim. Sci. 54:605.

Mueggler, W. F. 1965. Cattle distribution on steep slopes. J. Range Manage. 18:255.

NRC. 1981. Effect of environment on nutrient requirements of domestic animals. National Academy of Sciences. National Academy Press, Washington, DC.

NRC. 1984. Nutrient requirements of domestic animals. Nutrient Requirements of Beef Cattle. Sixth Revised Ed. National Academy of Sciences-National Research Council, Washington, DC.

Osuji, P. O. 1974. The physiology of eating and the energy expenditure of the ruminant at pasture. J. Range Manage. 27:437.

Parker, E. E., J. D. Wallace, A. B. Nelson and R. D. Pieper. 1974. Effects of cottonseed meal supplement and age of first calving on the performance of range cattle. New Mexico State Univ. Agr. Exp. Sta. Bull. 627.

Peterson, R. A. and E. J. Woolfolk. 1955. Behavior of Hereford cows and calves on short grass range. J. Range Manage. 8:51.

Rittenhouse, L. R., D. C. Clanton and C. L. Streeter. 1970. Intake and digestibility of winter-range forage by cattle with and without supplements. J. Anim. Sci. 31:1215.

Roath, L. R. and W. C. Krueger. 1982. Cattle grazing and behavior on a forested range. J. Range Manage. 35:332.

Shephard, J. H. 1921. The trial of the short grass steer. North Dakota Agr. Exp. Sta. Bull. 154.

Smoliak, S. and H. F. Peters. 1955. Climatic effects on foraging performance of beef cows on winter range. Can. J. Agr. Sci. 35:213.

Sneva, F. A. 1970. Behavior of yearling cattle on Eastern Oregon range. J. Range Manage. 24:155.

Stobbs, T. H. 1970. Automatic measurement of grazing time by dairy cows on tropical grass and legume pastures. Tropical Grasslands 4:237.

Stoddart, L. A., A. D. Smith and T. W. Box. 1975. Range Management (3rd Ed.). McGraw-Hill Book Co., New York.

USDA. 1981. SEA-AR Range Research Assessment, Western United States. United States Department of Agriculture, Science and Education Administration, Agriculture Research, pp. 5-13.

Wagnon, K. A. 1963. Behavior of cows on a California range. California Agr. Ext. Serv. Bull. 799.

Wight, J. R., C. K. Gee and R. J. Kartchner. 1983. Integrated rangeland and cropland management. In: H. E. Dregne and W. O. Willis (Ed.). Dryland Agriculture. Agronomy Monograph 33, pp. 435-460.

Wilson, P. N. 1961. The grazing behavior and free-water intake of East African shorthorned Zebu heifers at Serere Uganda. J. Agr. Sci. 56:351.

SELECTION OF RANGE CATTLE: CANADIAN VIEWPOINT

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Introduction

Thank you for giving me the opportunity to tell you about some of the beef cattle breeding work that has been conducted at our Research Substation on the shortgrass prairie near Manyberries, Alberta.

This meeting is particularly timely for me because we are currently reviewing the beef cattle research work across Canada at the Federal Government Stations and because I am now heavily involved in the administration of research, as well as in the research itself.

Earlier, we had discussions on the evolution and management of range grasslands and forage-animal interactions. Animal breeders, at any time, must consider the environment when planning projects and interpreting research results. But, seldom is the challenge of the environment a more important consideration than in a range environment when we are trying to select cattle for performance in environmental conditions that vary significantly from year to year - and often are suboptimal for beef cattle production.

The survival and consistent reproduction of our cattle has been the overriding factor in determining the direction of beef breeding research under Canadian range conditions. My topic is "Selection of Range Cattle" and I plan to look at it in terms of choosing individual animals or evaluating breeds or crosses that perform well under range conditions. When we are successful in selecting cattle that will perform under our specific range management conditions, I feel that we usually have cattle that are relatively efficient in production as compared to those raised where both pasture and winter feed are in abundant supply. Only scientists or producers who have raised cattle under range conditions can really know how remarkably tough a cow can be and how much - or sometimes how little - she really needs to eat in order to survive and to reproduce. The identification and provision of an adequate nutritional level, through pasture and perhaps supplemental feed, is the single most important factor in establishing the performance, or lack of performance, of many of the larger and heavier milking breed crosses that we have had access to in the last 15 years. I would like to pursue this interaction between the cows and the environment - from the cow's point of view because this session is about "The Cattle".

We are looking at the past, present, and future of range research so I feel that it is important that I bring to this meeting some idea of our Agriculture Canada Research Branch programs in range research at the Manyberries Substation and express a few facts and opinions based on those programs.

A range environment means different things to different people, so I feel that we should define the environment that we are talking about. My range environment is located along the U.S.-Canada border about 40 miles north of Havre, Montana. The ranch, near Manyberries, consists of 42,000 acres, about 36,000 of which is short-grass prairie and 6,000 is seeded Russian wild rye. Precipitation averages 11 inches per year. Predominant native range species include blue grama and wheatgrass, with moderate amounts of June-grass and needle-and-thread grass, along with sage and cactus. The native range is rated at 60 acres per cow - or 5 acres per cow per month - for grazing lease purposes. Put in other terms, pounds of dry matter per acre range from less than 300 to over 800, with an average of about 380. However, we are below the average forage production in 2 out of 3 years and the larger exotic crosses require far more than the 5 acres estimated for British breeds so that I don't feel that existing recommendations are current for our conditions and the cattle types we now have available. The work being done by Chris Havstad at M.S.U. on forage consumption by range cows may shed some light on our problems. We are currently looking at incorporating a similar technique into a new project. The Russian wild rye pastures, used primarily in the spring and early summer, have two to three times the carrying capacity of the native range. Winter shelter consists of coulees in Lost River Valley. No trees or constructed shelters are available on winter or summer range. Temperatures range to -40°F, but sometimes a significant stress can be derived from what we call chinook winds - warm winds that come through the Crowsnest Pass of the Rocky Mountains and raise the temperature by as much as 70° in a few hours. Problems with the environment are behind many of our decisions for range research. Projects have ranged from the evaluation of several breeds and crosses for productivity in different environments, to long-term selection studies involving single trait selection and genotype-environment interaction, to the selection and comparison of strains from straightbred and crossbred lines.

Past Research

Cattalo (Domestic x Bison Crosses) Evaluation. In 1950, a herd of bison and bison x domestic cows, mostly 25 or 50% bison developed at another ranch, was transferred to Manyberries. Under that rigorous range environment, with only Lost River Coulee as a winter shelter, the herd was to undergo selection that would produce a hardy animal with good meat qualities.

The Canadian Government had become involved with the concept of crossing bison and domestic cattle in 1916. Losses in range cattle herds had been extensive during many winters in the late 1800's and early 1900's. Ranchers had observed the hardiness of the bison and had attempted to cross the bison with the domestic cattle to incorporate hardiness into the range herds. Essentially, the period from 1916 to 1950 involved various attempts to produce the cross. At one point, even the Yak was incorporated. The problems were many. Some bison would not produce when moved to a new location. Bison and domestic animals would not associate with each other and, therefore, seldom mated. That problem was circumvented by raising bison bull calves on domestic cows. Several attempts to mate bison bulls with domestic cows resulted in less than 10% calf crops and many dead cows, because the cows suffered from dropsy and aborted their calves at 8 months. The reverse

cross – domestic males on bison females – was relatively successful but progress was slow because bison cows were not available in large numbers. Performance selection was minimal before 1950, it was more a matter of retaining survivors.

At Manyberries, a higher percentage of Cattalo cows than British breed cows grazed during severe winter weather. Cattalo haircoats were thicker and heavier than those of domestic breeds. Male Cattalo were sterile until the proportion of bison was reduced to 3/16 by backcrossing. Cow herds that were 50% or 25% bison produced about 20% fewer calves than contemporary Herefords. Relatively consistent reproduction was achieved with a cow herd averaging 14% bison but the performance of their progeny in terms of growth rate and carcass quality did not exceed that of the Hereford. The population did respond to selection for growth rate but was not superior to other crosses now available. At that time (1965), most of the problems had been identified. While we felt that the herd would perform well in a northern environment, no northern location was available to transfer the herd to and the Cattalo were disposed of to make room for other research. Our experience was that productive cattle could be developed from this rather wide species cross, although the problems were many. We don't require hardiness (survival) to the same extent as we used to because herds are better cared for. From a beef production standpoint, newly available crosses will outproduce bison crosses in most range environments. Where conditions are extremely rigorous and hardiness for survival is a definite requirement, we recommend the use of straight bison rather than bison crosses.

Scotch Highland Evaluation. From the mid-1950's to mid-1960's, Highland and Hereford cattle and their reciprocal crosses were evaluated for hardiness and productivity under range conditions. The primary reason for selection of the Highland was its long and heavy haircoat – and the breed's apparent hardiness in the damp, mountainous regions of Scotland to which it was native. Steers were evaluated through feedlot and carcass studies. Female progeny were retained as cows. Highlands could not be recommended as a pure breed under range conditions. Although, as mothers, they had a very high survival rate of progeny from conception to weaning, progeny lacked growth rate and the ability to achieve an acceptable market finish. The haircoat did not provide a significant advantage for the Highland. Reciprocal-cross calves had excellent growth and were comparable to the Hereford in carcass quantity and quality. Crossbred dams produced more calves and more milk than either breed of parent and were excellent range cows. Highlands have performed well on the slopes of the Rocky Mountains and have shown preliminary promise in Northern climates where their haircoat may be beneficial as a protection against black flies.

Brahman-Cross Evaluation. Brahman bulls were mated to Angus, Shorthorn and Hereford cows in the early 1950's at Manyberries and were kept to the early 1970's. A prime example of hybrid vigor was the Brahman x Shorthorn cross. Neither parental breed was particularly hardy in the Manyberries winter environment, but that cross was the most productive of the three crosses in terms of progeny performance. Brahman crosses were well suited to the Manyberries range. They conceived easily, were good mothers, although somewhat temperamental, and consistently produced good weaning weights. A

notable observation that has not been taken sufficient advantage of was that, although the development of the first cross resulted in an increase in birth weight, the first-cross cow herself tended to produce a smaller calf. A sample of 20 Brahman x Hereford cows was compared to 20 Hereford cows in lifetime productivity. Cows were 16, 17 and 18 years old when the last Hereford was eliminated and four crossbreds remained. The Brahman crosses produced 26% more calves and 52% more pounds of beef to weaning than the Herefords and, although their disposal rate paralleled that of the Herefords, the lag time was about 4 years. We proved under range conditions what others were finding basically with the British breeds, that conception, mothering ability and weaning weights could be improved by crossbreeding. As we will see later, these well-known facts did not hold true when the exotics came on the scene after 1965.

Selection from Crossbred and Straightbred Bases. A cooperative project was entered into with a rancher near the Manyberries Substation. The rancher's aim was to develop a more productive strain for range conditions than the predominant Hereford. The aim of the researchers was to establish the immediate response from crossing and the long-term response to selection for yearling weight in lines emanating from straightbred and crossbred bases.

The base population for both lines was a Hereford cow herd that because of its treatment had essentially undergone natural selection for several generations. Those cows were mated to Brown Swiss, Holstein, and Red Angus males to form the first-cross males and females that would be the basis of a crossbred line. Initially, crossbred bulls were longer, leaner, and 10% heavier than Herefords when slaughtered. Crossbred heifers showed superior growth rate and comparable hardiness. As cows, the crossbreds produced calves that were about 30% heavier at weaning and had up to 10% more feedlot gain than the Herefords. Udder troubles were not significant, nor was hardiness, if reasonable winter supplementation was provided. The project was terminated following 15 years of cooperation. Evaluation of the performance difference between straightbred and crossbred lines is continuing. The obvious success of the crossbred line, which included crosses not normally hardy under extremely rigorous conditions was, in my opinion, due chiefly to the highly adapted, naturally selected cow herd on which both lines were based.

Current Research

Foreign Cattle Breed Evaluation (FCBE). The opening of quarantine stations in 1965 allowed Canadians to import cattle directly from continental Europe. The response of these cattle to the Canadian environment was unknown. Available information was biased or not applicable. Thus, in 1969, the Research Branch of Agriculture Canada began a four-phase program to evaluate, in an objective comparison, the most predominant and promising of the "newly imported" foreign breeds of cattle in a crossing program. The FCBE program involved Howard Fredeen and Jack Newman at the Lacombe Research Station, Gunther Rahnefeld at the Brandon Research Station, and myself at the Lethbridge Research Station—working out of the Manyberries Research Substation.

In the first phase, from 1970 to 1972, cooperating ranchers produced 10 specific types of first-cross heifers; the Hereford-Angus and nine crosses

sired by Charolais, Limousin and Simmental and out of Angus, Hereford and Shorthorn dams. The 1,150 heifers we developed to breeding age, and feedlot and carcass data were obtained on the contemporary male progeny.

In the second phase, at 14 months of age, the heifers in each cross were divided equally between the extensive range environment at the Research Substation near Manyberries and the semi-intensive cultivated pasture environment near Brandon, Manitoba.

The Manyberries experiment has already been discussed.

At Brandon, cattle grazed cultivated grass through spring, summer and fall and were confined for winter feeding on corn or barley silage.

Yearling heifers were bred to Red Angus or Beefmaster in an attempt to promote easier calving. Second and subsequent calves were sired by Charolais, Chianina, Limousin, or Simmental bulls. All calves were three-way crosses.

Each breed cross of dam was evaluated for reproductive capabilities--ability to conceive, number of services, calving difficulties, and for the growth and carcass characteristics of its calves produced over a 7-year period (in excess of 4,000 calves).

Obviously we can't discuss all of the results. Five research bulletins were published on preliminary results and, to date, nine scientific articles have been published in the Canadian Journal of Animal Science since 1980. Other analyses are still underway, including an economic analysis.

What kinds of lessons did we learn - besides the ones of breed-cross comparisons? When breeding yearling, exotic-cross females to produce three-way-cross calves, the careful choice of bull and breed of bull can make a very great difference to calving difficulties - but they still will be significant - because hybrid vigor is maximized and 1/2-exotic heifers try to produce a big calf. Because of nutritional restrictions, the same crosses produced calves that were 8% smaller at weaning under range conditions than under parkland conditions where feed was abundant. An extension of that problem exists with the larger exotic crosses, particularly the Simmentals. Because of their own size and milking ability, where feed is restricted under range conditions (particularly years of below average forage production), they apparently cannot consume enough feed to maintain their own condition and, therefore, will not rebreed. That problem reduced the advantage that exotic-cross females had over the Hereford-Angus cross as we went from the parkland to the range environments. Also (see table 1), whereas the Simmental-cross cows had the best lifetime productivity at Brandon in the parkland conditions, the Charolais-cross cows had the best productivity under range conditions, primarily because they produced 6% more calves to weaning. These are serious problems - because cattlemen are choosing or are being advised to raise high-producing cattle in marginal areas - and they don't have the management expertise to cope with the problem or, alternatively, the right cattle for the environment. Two ways that we are trying to look at the problem are (1) to establish [in Phase III of our project] the nutritional requirements of the various exotic crosses, and (2) to look at 1/4-exotic cows compared to 1/2-exotic cows in Phase IV

TABLE 1. RELATIVE RANKING† BY BREED OF SIRE (C, S, L) AND BREED OF DAM (H, A, N) OF FIRST-CROSS FEMALES FOR SEVERAL COMPONENTS OF REPRODUCTIVE PERFORMANCE

	Brandon					Manyberries				
			Production per opportunity					Production per opportunity		
Breed cross††	Total cow losses of potential years (%)	Years in herd as a percentage of potential trial years (%)	Conceptions (%)	Calves weaned (%)	Weight of calf (kg)	Total cow losses of potential years (%)	Years in herd as a percentage of potential trial years (%)	Conceptions (%)	Calves weaned (%)	Weight of calf (kg)
HA	22.7	88	82.5	77.0	154	30.7	84	79.0	72.1	124
C	20.0	91	86.2	80.1	176	26.3	88	83.6	74.9	143
S	28.4	89	84.0	79.9	181	34.9	84	76.8	69.0	139
L	33.5	86	82.1	75.8	161	34.3	81	74.8	66.4	125
H	28.8	89	82.6	78.6	171	33.7	84	76.1	68.2	133
A	21.6	92	84.0	78.4	172	24.1	88	79.1	72.5	139
N	32.0	84	84.9	78.4	176	38.3	81	79.0	69.3	135

† Underlined figures identify the top-ranking performance for the groups of sire crosses and dam crosses.

†† Breed codes: C = Charolais, S = Simmental, L = Limousin, H = Hereford, A = Angus, N = Shorthorn.

of the project, to see if we can get consistent reproduction and increased lifetime productivity from the 1/4-exotics. That Phase will be completed in 1986.

The exotic crosses have changed the rules, we can no longer expect that crossbreeding will assure fertility or that first crosses will outperform backcrosses.

Phase III of the FCBE project was designed to answer an obvious question. What is the energy requirement for the maintenance and relatively high production achieved by some of the exotic crosses? In a 4-year study, energy inputs were measured for each breed cross for (1) maintenance during the period from weaning to the following calving (about 150 days), and (2) lactation during the portion of the suckling period (about 90 days) from about mid-June to the mid-October weaning. The ration was adjusted for each breed cross at 28-day intervals based on changes in weight and ultrasonic backfat measurements. During the lactation portion, milk production was assessed on cows both in the feedlot and under range conditions.

The diet at Manyberries was based on a 70% alfalfa:30% wheat straw cube containing about 16% protein; while at Brandon, the diet was based on corn and barley silage.

I consider Phase III to be a very important data bank. Although it is not yet published, I have a few observations that you might find interesting.

When they come off the range at weaning in October, our various exotic cross groups that have weaned calves will measure 2 to 5 mm backfat with Hereford-Angus in the 8 to 9 mm range. Many individual cows will have no measurable backfat. We have been measuring backfat between the 11th and 12th rib with an ultrasonic instrument, and I believe that it is extremely accurate on low fat levels. In my opinion, backfat levels are a good measure of cow condition. Eyeballed condition scores are not satisfactory for our work where most cows are thin. I do not believe that we need to consider internal body fat when measuring condition. Backfat is both an insulator and a source of energy for the cow. In my experience, thin cows should be increased to at least 5 mm of fat as soon as possible after weaning or they could have trouble competing for feed, surviving in cold winters or rebreeding the following summer. The amount of energy required to achieve this 5-mm level and maintain it has been as much as 50% more for at least a portion of the winter period than would be recommended in NAS-NRC guidelines for cows of a given weight. When cows are very thin, it is too late to increase the feeding level. Digestibility of feed can be reduced in very cold weather and cows will often lose their desire to compete for feed. Besides being a source of insulation, backfat is also the most easily accessed source of energy for the cow.

Selection for Feedlot Gain on Two Diets. In 1963, two 108-cow (calving) lines were formed at Manyberries within each of the Hereford and Angus breeds; and the lines closed. Breeding replacements are selected on the basis of superior gain in the 168-day period immediately following weaning. Progeny from the first line of each breed are fed a high concentrate diet (60% barley, 10% oats, 10% beet pulp, 20% chopped hay) during that feedlot

period. Progeny from the second line of each breed are fed a diet of 100% chopped alfalfa. The 168-day feedlot period is the only time that lines are treated differently. After 1 year of age, all cows are run together.

The project objectives are to assess the long-term (20 years or 5 generations) effect of selection for 168-day postweaning gain, the influences of two levels of nutrition (80% concentrate:20% alfalfa vs 100% alfalfa) on that selection, and the correlated response in other traits.

Most of the digestive disturbances and deaths (predominantly bloat), and all of the founders during the feedlot test occur among calves fed the concentrate diet. Selected bull and heifer calves can be used for breeding at 14 months.

Calves in the roughage-fed lines tend to gain faster to weaning than calves from the concentrate-fed lines. After about three generations of selection, milk production and the amounts of fat, solids-not-fat, and protein were significantly greater in the roughage- than in the concentrate-fed lines. Perhaps cows fed as calves on roughage are more efficient or perhaps the udders of cows fed on 80% concentrate as calves have been deleteriously affected by the concentrate diet.

Hereford bulls continued on the concentrate diet to 20 months were shown by Glenn Coulter, Reproductive Physiologist, to have a 50% reduction in epididymal sperm reserves and a higher percentage of abnormal sperm. More recently, a deleterious effect has been demonstrated in 15-month-old bulls.

Damage to the rumen wall has been demonstrated by K. J. Cheng, Microbiologist, in animals that receive the concentrate diet. The speculation is that the damaged areas are the routes by which harmful bacteria from the rumen can attack the liver to cause abscesses.

The last calf crop was selected this spring, following 19 years of selection on 350+ calves per year. Lines will now be compared (between and within) by feeding half of the calves of each line on each diet in individual feeding facilities. Heifers will be retained for milking as 2-year-old cows to determine which of diet or selection has influenced milk production. Efficiency of feed utilization during the winter maintenance period of cows will be assessed to determine how lines differ as a result of long-term selections (five generations) on two diets. One of the more significant conclusions is that it is neither necessary nor wise to select replacement males or females on a high energy diet.

Future Research

Our current thrust reflects our interests in using a multidisciplinary team approach to identify the important traits of reproductively efficient cows and bulls. The numerous objectives are outlined in a new project that will be conducted in the two previously described environments at Brandon and Manyberries.

Currently the team includes three beef breeders, a reproductive physiologist, a cow-calf nutritionist, a range production specialist, and an

economist — each participating in the development of the plan and each contributing to the assessment of what factors affect cow efficiency and how important they are.

The cow herd, when established, will fluctuate between 500 and 800 cows at each location. The foundation cows were those that produced the most pounds of calf weaning weight during their first eight calving opportunities on the Foreign Cattle Breed Evaluation project.

The original populations were genetically very similar at Brandon and Manyberries on the Foreign Cattle Evaluation project. They were produced in the same herds and sired by the same sires. But, because of the pressures of the environments, natural selection has had a hand in identifying different parts of the two populations as the top producers in the two environments. From the breeders' standpoint, we are interested in maintaining the integrity of the Brandon and Manyberries populations, intermating the various contributing breed crosses at each location to establish one breed composition within each population and exchanging portions of each population between the Brandon and Manyberries environments to study genotype x environment interaction effects. All heifers produced on the project will be retained for breeding and all bulls retained to 15 months of age. This will allow us to follow the reproductive and growth performance of both sexes, and correlate reproductive traits between relatives. Milk production, efficiency of feed utilization (feed consumption in feedlot and on range), and cold tolerance (using telemetry), of cows will be assessed. All reproductive variables on males that have a chance of being useful in bull evaluation and selection will be measured — such as weight, backfat, scrotal measurements, consistency and shape of testicles, libido, dominance, semen evaluation, and temperature in and around the scrotum using infrared thermography techniques. Onset of first estrus, return to estrus, and complete calving and growth records of females and growth and carcass traits on bulls will be taken.

The nutritionist will measure the Cu, Mb, Zn, and vitamin A interrelationship and their correlation to reproductive performance. The pasture expert will measure the pasture influence and the economist will put a dollar value on the results (an area that has received far too little attention in most animal work). We want to stress an integrated approach rather than just having five or six scientists using the same animals.

We hope to identify what factors are important in reproductive efficiency and growth in the two environments and develop or identify some of the better predictors of that performance for more accurate selection of breeding animals. The design of the project also makes possible the study of a large number of other side issues.

As a final comment, I recommend that we organize visits between animal scientists at the Lethbridge Research Station and those at Miles City and Montana State University. We have much common ground in our interests, our environments and our problems. I can foresee that information exchanges could be extremely beneficial to researchers at each location and that those exchanges could lead to cooperative working arrangements in the future.

RANGE COW SIZE

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Cow size in the northern range area has typically been larger than in the eastern and southern areas of the country. This larger size has evolved from the cattleman's observations that these cattle performed best for him rather than a specific recognition of the thermoregulatory advantage of large size. The latter is primarily conditioned by lower weight-specific energy consumption.

Thirty years ago, when small cattle were popular, the range cattleman did not turn to the extreme small size popular elsewhere; thus, the range country was able to provide much of the breeding stock needed when larger size again became popular. It appears the range area in general is not following the swing of the pendulum toward larger size to the extent of cattlemen in other areas. Further, it appears that the range area has been a stabilizing influence in the wide swings of cow size during the past 40 years. Cow size has changed in the range country during this period but not to the extremes found in other areas.

My assigned topic overlaps several other topics on the program, but I have made a special effort to deal with aspects specifically related to cow size and those I feel the other speakers may not deal with. The areas I will discuss are efficiency, crossbreeding systems and reproduction as related to cow size.

Cow Efficiency

At the outset, I will briefly summarize our own research in this area. In 1968, 90 grade Angus weanling heifers and 90, 3/4 or higher percentage Charolais weanling heifers were purchased and used to produce the foundation for our first-phase cow efficiency research. These heifers came from 59 different herds in South Dakota and should have represented a broad sampling of the genetic variation available. Since we could not obtain such a broad sampling on the sire side, genetic variation was controlled by breeding to one Angus bull and one Charolais bull to produce three calf crops. Matings were made to produce straightbred Angus, straightbred Charolais and the reciprocal crosses (table 1). Heifers were randomly allotted to two groups. One, a drylot management group where energy intake of the cow and calf could be measured for the cow year, and the other, a pasture group managed under typical cow-calf production systems. The performance of the cows on the pasture system was used to determine the energy intake of their contemporary half-sibs in drylot. Calves were allowed to nurse morning and evening at the times the cows were individually penned and fed. Calves remained in the pens overnight with access to creep feed. Energy intake of the cow and calf was thus measured for the cow year (weaning to weaning) and efficiency expressed as weaning weight of the calf divided by TDN consumed by the cow and calf. As the table indicates, no important differences were found between breed groups, and other analyses indicated no effect of cow size on

TABLE 1.   LEAST-SQUARE MEANS FOR COW EFFICIENCY IN PHASE 1

Breed group	Phase 1 N	Efficiency WW/TDN
AA	103	.091
AC	73	.090
CA	89	.091
CC	68	.089

cow efficiency (R^2=.01).   This study was continued through 1979 at which time cows remaining in the project had had an opportunity to produce eight calves.

Phase 2 of the project was initiated in 1978 resulting in a 2-year overlap of the two phases.   An ongoing crossbreeding experiment at our Antelope Range Livestock Station provided straightbred Hereford and Simmental x Hereford and Angus x Hereford crossbred groups which were used to study the heritability of cow efficiency and possible predictors of cow efficiency. We have not found significant or important differences in efficiency among these breed groups (table 2).

TABLE 2.   SUMMARY OF PHASE 2 COW EFFICIENCY LEAST-SQUARES MEANS TO DATE

Breed group	Phase 2 N	Efficiency WW/TDN
Hereford	43	.078
Simmental x Hereford	87	.080
Angus x Hereford	36	.081

The results of phase 1 and summaries of phase 2 appear to be in agreement with other published reports dealing with cow size and breed difference effects on cow efficiency where (1) the annual energy intake for the cow and calf has been measured, (2) the output resulting from that energy input has been measured, and (3) the cow has been fed sufficient energy to maintain reproduction.   These experiments have been conducted in environments ranging from Texas into Canada and with a variety of methods used to determine intake level of the cows.   The cow has indicated a marvelous ability to adjust her output to the energy input provided.

Recently, a good deal of attention has been given to maintenance require-ments. In some cases, the implication, whether intended or not, seems to be that since smaller cows have lower maintenance and thus lower input they automatically have an advantage either in efficiency or economics. However, lower input means lower output as evidenced by the lack of difference in cow efficiency due to cow size.   The concept needed is that a given energy supply associated with any particular ranch unit can be used to optimize the operation. If we move to large size cows, we then must reduce the number of cows in relation to the carrying capacity of the unit with smaller cows.

With no other variables involved other than cow size, the available evidence on efficiency would indicate no difference in output due to the change in cow size. The larger cows require more energy but, at the same time, produce more output. The limitation is that size cannot be increased beyond the ability of the range to provide energy to maintain reproduction.

There are other concerns about maintenance that are involved in considerations of efficiency related to size and/or milk production of different breeds available for use in crossbreeding systems. In reading reports and listening to talks, I sometimes get the feeling that all we have to do is lower maintenance through selection or by some other means and we will have a more efficient and economical cow. I emphasize that this is my reaction and it may not be the intent of the authors. If that is the intent, it overlooks the matter of voluntary feed intake. The turning of the rheostat that lowers maintenance probability will not simultaneously adjust the physiological (distension) limiting switch on voluntary feed intake. For range cows, the chemostatic switch would not be expected to apply and, for the northern range, we would not want to influence a change of the thermostatic switch. The result, as I see it, would be an increasingly fatter cow as we turn down the maintenance rheostat. Simultaneous control of the voluntary feed intake along with the lowering of the maintenance requirement would be beneficial if one could exercise precise enough control to keep the animal adapted to its environment.

Another consideration of maintenance is method of estimation. Nutritionists prefer an open, nonlactating female--even though we know that changes in physiological state change maintenance level. Open and dry cows are not present in a well-managed beef herd and do not make up a major proportion of even a poorly-managed beef herd. Since gestation and lactation will change maintenance requirements, maintenance based on the open, dry cow has little utility. One further problem with the usual method of estimating maintenance is that of using three planes of nutrition and combining the results into one measure of maintenance. Since maintenance can change with plane of nutrition, this appears to be much like averaging the simple effects to obtain a main effect in the presence of an interaction, which is not a valid procedure.

I believe the multiple regression procedure of separating maintenance, weight change and lactation requirements provides a simultaneous estimate of all parts subject to the same environment, the same physiological state, the same genotypes and the same plane of nutrition. Table 3 contains our estimates of this kind of energy partition for three periods during the cow year. It emphasizes how biological types differ in how they partition energy to the various needs. This type of energy partition from our first phase (Anderson et al., 1983) predicted within 6% the energy consumption of a group of Hereford cows on experiment in Wisconsin (E. R. Hauser, personal communication).

Crossbreeding Systems

A common recommendation in recent years for crossbreeding systems has been to breed a high growth potential bull to small cows. More specifically,

TABLE 3. PREDICTION EQUATIONS FOR TDN REQUIREMENTS FOR THREE PERIODS OF THE COW YEAR FOR ANGUS X HEREFORD AND HEREFORD COMBINED AND SIMMENTAL X HEREFORD GROUPS

Breed group	Intercept

Midgestation

AxH&H	Period TDN = 123.829 + .639 (MWT)[a] + .581 (WTC)[b]
SxH	Period TDN = 128.059 + .527 (MWT) + .633 (WTC)
SxH/AxH&H	.82 1.09

Last trimester

AxH&H	Period TDN = 187.177 + .649 (MWT) + .367 (WTC)
SxH	Period TDN = 241.463 + .540 (MWT) + .298 (WTC)
SxH/AxH&H	.83 .81

Lactation

AxH&H	Period TDN = 682.601 + 1.537 (MWT) + .2990 (WTC) + 54.920 (LACT)[c]
SxH	Period TDN = 703.746 + 1.725 (MWT) + .2820 (WTC) + 45.436 (LACT)
SxH/AxH	1.12 .94 .83

[a] Maintenance weight.
[b] Weight change.
[c] Milk production—average of four daily measures.

breeds with high maternal potential are crossed to produce cows which, in turn, are bred to bulls high in growth potential and carcass merit. Data collected in the first phase of our project offer the opportunity to evaluate if this recommendation should be restricted to small cows or if cows of varying size but with equal maternal ability could also be used. Table 4 indicates the distribution of phase 1 cows with respect to year, age and breed of sire to which they were exposed. All cows within a year were bred to one sire. Because there were heifers calving for the first time in each of the first 3 years, the Polled Hereford bulls were chosen for smaller size and lower growth potential. The 4 years in which Polled Hereford bulls were used formed the low-growth-potential sire group. In the remaining 4 years, a Limousin and Simmental bull were each used 1 year and two Salers bulls were each used 1 year. This group formed the high-growth-potential sire group. The small- and large-cow-size groups were formed by dividing the cows in all four breed groups on the basis of the average weight of the Angus cows. All cows below 437 kg were designated small and all above that weight large. The model used (bottom table 4) included the main effect of sire group, cow size, sex, year-within-sire group, interaction of cow size with sire group and covariates for cow condition at calving, cow condition at weaning and weaning age. A dependency existed between age of dam, year and sire group. Since age of dam did not account for substantial variation in cow efficiency in this data set (Buckley, 1982), it was dropped from the

model. The results indicated that all three covariates were significant along with the effects of sire group, sex and year-within-sire group. The least-squares means for the simple and main effects involved in the cow size x sire group interaction indicate the lack of cow size effect and the important effect of growth potential of the sire (table 5). There was no evidence of an interaction between the two. In order to gain evidence as to the biological basis for the sire group effect, the same model was used with milk production as a dependent variable. Again, the cow size and interaction of cow size with sire group effects were not significant. The sire group effect was .6 kg per day increase in milk production (P<.001) resulting when cows were bred to high growth potential bulls. Part of this increase could be age-of-dam effect; however, a part of the age-of-dam effect should be removed with the year-within-sire-group source of variation. It may be worth emphasizing that these results are based on the same cows bred to the two different kinds of bulls free of the effects of confounding of growth potential of the sire and growth potential of the breed of sire and free of any differences in heterosis level in the calves.

TABLE 4. NUMBER OF OBSERVATIONS PER YEAR, AGE OF DAM, BREED OF SIRE SUBCLASS AND MODEL ANALYZED

Year	2	3	4	5	6	7	8	9	Breed of sire
1972	31								PH
1973	16	20							PH
1974	19	16	20						PH
1975		20	14	19					Sa
1976			16	15	21				Li
1977				19	12	17			Si
1978					14	10	15		PH
1979						13	8	11	Sa

(Header spanning columns 2–9: "Age of dam")

Model

$$Eff = SG^* + CS + Sex^* + Yr: \quad SG^* + CS \ x \ SG$$

$$+ \ b^*_{ccc} \quad + \ b^*_{ccw} \quad + \ b^*_{wa}$$

* P<.001.

It has been suggested that these results are negative to use of a terminal cross. Given that these results are confirmed in other experiments, I would interpret them to mean large cows can also be maternal if they have the milk production and are fed sufficient energy to reproduce. Cow size should not then be part of the definition of a maternal breed or cross. This generally leads to the question, do I argue the term complementarity? While I don't see the need for it, I certainly have no argument with others using it. At

this point in time, the use of it would probably perpetuate the concept of small cows being more efficient.

TABLE 5. LEAST-SQUARE MEANS FOR SIMPLE AND MAIN EFFECTS OF GROWTH POTENTIAL OF SIRE AND COW SIZE GROUPS FOR COW EFFICIENCY

	Low growth sire WW/TDN	High growth sire WW/TDN	
Small cow	.086	.092	.089
Large cow	.088	.093	.090
	.087	.092	

Some writers suggest that using large breeds with small breeds in rotation crossbreeding systems will not work because of the disparity in mature size. Our Simmental x Hereford, two-breed rotation has worked well for the past 9 years, as you will see in the poster session this evening. We have commercial producers all across South Dakota who have been successful with two- and three-breed rotations involving large breeds and for a number of years. Part of the explanation is that the crossbred cows do not attain the large mature size of the purebred cows of the large breed. Perhaps part is due to some of the misconception regarding the effect of large cow size just discussed. The adverse effects of underfeeding large cows to the point that they do not reproduce has influenced some of these recommendations.

The preceding discussion leads some people to conclude that there are no individual differences in cow efficiency and that nothing can be done about improving it. Our experience indicates that there is fully as much variation available in cow efficiency as was available in weaning weight at the time we first started working with that trait. Buckley and Dinkel (1981) indicated that the repeatability of the two traits are equal. Further, there does not seem to be any evidence of heterosis for cow efficiency. These considerations coupled with the relatively high accuracy (R^2=.79) of our prediction equation for cow efficiency (Dinkel and Jost, 1984) would indicate an opportunity to improve the trait at near the same rate as improvement has been in weaning weight. This would require forming contemporary groups of cows considering not only the usual season, sex and creep differences but also breeding value of sire, breeding value of the breed of sire and heterosis level of the calf. If the equation is to be used to compare cows with different sex calves, our data show heifer calves to be 8.5% less efficient than bull calves. This would be a program primarily for breeders of registered cattle that would allow commercial producers to select their replacement bulls on the basis of their expected transmitting ability for cow efficiency as they now do for growth and maternal traits.

Reproduction

The effects of cow size on reproduction appear to fall into two major categories. The first is that of the necessity to maintain the plane of nutrition high enough to maintain reproduction in the larger animal. The second is the matter of dystocia, which I prefer to categorize as calf survival — and not part of the reproductive process. Since it is usually included with reproduction, I will follow the precedent.

Considering the rather large press that dystocia has received in recent years, I think it is important to separate what happens in a population that is static for mature size and where there is selection for rapid early postnatal growth vs what happens to dystocia in a population that is in the process of changing from small to large mature cow size. In the latter case, bulls of large mature size may be mated to rather small cows and, in some cases, the dystocia resulting from this kind of mating has been credited to what one might expect from selection for rapid early growth. In my opinion, the extreme emphasis on mature size and frame score in the selection of breeding animals in the British breeds has led to substantially more dystocia than that which would result from selection on early growth. In addition, we now have less opportunity for commercial producers to utilize smaller British-breed cattle with rapid early growth along with the larger breeds to build more flexibility into their crossbreeding programs. Not all breeders of British cattle have followed the mature size route; thus, some of the germ plasm with lower mature size potential is still available.

I have one final comment pertaining specifically to the northern range climate. Proper winter cow condition is required to stand the stress of extended periods of extreme low temperature or of blizzards that last for several days. While larger cows have the thermoregulatory advantage, they cannot be expected to stand these extreme climatic conditions without a layer of fat to provide insulation and an energy reservoir. This has been discussed previously this morning and I only want to emphasize the importance of this for this region of the country.

Literature Cited

Anderson, V. L., Lorna Jost, C. A. Dinkel and M. A. Brown. 1983. Prediction of daily total digestible nutrient requirement of beef cows in northern climates. J. Anim. Sci. 56:271.

Buckley, Brent A. 1982. Repeatability of cow efficiency, weaning weight and milk production in Angus, Charolais and reciprocal cross cows. M.S. Thesis. South Dakota State Univ., Brookings.

Buckley, B. A. and C. A. Dinkel. 1981. Repeatability of efficiency, weaning weight and milk production in Angus, Charolais and reciprocal cross cows. J. Anim. Sci. 53(Suppl. 1):136.

Dinkel, C. A. and L. K. Jost. 1984. Prediction equations for cow efficiency. J. Anim. Sci. 59(Suppl. 1):183.

MATING SYSTEMS FOR RANGE CATTLE

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Introduction

Upon reading the title for this presentation, one may legitimately wonder whether mating systems are different for range cattle than other types of cattle and other species. The answer is yes and no. Inbreeding is obviously inbreeding and crossbreeding is obviously crossbreeding, but I believe that our orientation needs to change as we think about mating systems for range cattle.

Much of what I say will be based on fact. However, speakers were urged to emphasize opinions, concepts, ideas and hypotheses; and as a result, some of what I say will be based on speculation. Therefore, this presentation is not intended as a complete literature review because I wanted to stress some concepts and because good literature reviews have been published (Mason, 1966; Cundiff, 1970; Long, 1980).

The objectives of this presentation are to focus on: (1) some general statements and thoughts regarding the interaction and(or) relationship of mating systems and the range environment; (2) a brief discussion of crossbreeding systems primarily as they relate to management under range conditions; (3) the dominance model for heterosis which will be discussed starting at a fairly basic level in order to provide a framework within which to work; (4) some results from a crossbreeding project carried out under range conditions at the Northern Agricultural Research Center (NARC) near Havre, Montana; and (5) some speculation will be done.

General Statements and Thoughts

In the future, most commercial cows managed under range conditions will be crossbreds. This has been the trend for the last several years, and I believe the trend will continue until a very high percentage of cows under range condition will be crossbreds.

Crossbreeding is more useful to beef cattle breeders in a range environment than to beef cattle breeders in most other environments. Range environments vary tremendously, but crossbreeding allows the breeder to produce a unique crossbred genotype to fit each environment. The idea of matching genotype to environment takes on special significance when cattle are under range conditions because range conditions tend to be stressful environments and are so varied (not only from ranch to ranch, but also from year to year for the same ranch and from season to season for the same year and ranch).

The perfect match of genotype to environment may not be a particularly easy thing to do. However, it should not be too difficult to make a reasonably successful match. A perfect match would optimize cow productivity in the average year according to one definition. However, some ranges may be below

average in 2 out of 3 years. Hence, the perfect match may result in low reproductive rates during some years and increase the amount of risk for an operation. As a result, it may be more advantageous for the cattle breeder to make a reasonable match of genotype to environment. That is to say, the reasonable match allows for enough cushion (or biological resilience) so that in years when the range conditions are below average, the majority of the animals will still reproduce.

Are some genotypes more adaptable to a variety of range conditions? Perhaps adaptability is one reason we observe heterosis. A related hypothesis is that the more extensive range conditions are able to support a smaller range of genotypes than more favorable environments.

We all know that fat production is inefficient. Or is it? When cattle are maintained under range conditions, the cow that has the ability to store fat during certain times of the year and mobilize the fat in other times of the year may be the more efficient. Cows that are able to store backfat more readily may also have an advantage in those range environments where cattle are exposed to cold stress during the winter months.

Animal breeders need to do a better job of describing the range environments under which experiments are conducted because experimental results may change from environment to environment. It is extremely important that we accurately describe the range environment to allow proper interpretation of our results from experiments on mating systems. I believe that there are some researchers who do not appreciate the extremes that cattle encounter in range environments. I stand in awe of our beef cattle in range environments when I think about the level of productivity that producers have come to expect from cattle and the environment in which cattle are expected to achieve this level of productivity.

It is important that we move the lab to the field. What I mean by this is that animal breeders, range scientists and range nutritionists need to work together to collect data that we have heretofore neglected to collect. We need to know how much and what cows and calves eat on the range, and we need to know how intake relates to breed group comparisons and results from different mating systems. We need to know more about grazing behavior and how it relates to mating systems. The cow that brings in the heaviest calf may not use the range in the most efficient manner. She may just be the boss cow that uses the creek bottoms, and she may be teaching her heifer calf to do the same thing.

Crossbreeding Systems

I agree with Baker (1982) that there is a tremendous need for education of commercial breeders in the area of crossbreeding systems--but I will not attempt to review all the various systems here. The following brief comments relate to crossbreeding systems for the range environment.

Table 1 shows a comparison of different crossbreeding systems. Dickerson (1974) concluded that the rotation-terminal system would probably be the most efficient system, and this was later substantiated by Notter et al.

TABLE 1. COMPARISON OF CROSSBREEDING SYSTEMS[1]

Type of system	Advantage
Static – terminal:	20%
Rotation:	
2-breed	16%
3-breed	20%
Rotational – terminal:	
2-breed	21%
3-breed	24%
Synthetic:	
2-breed	10%
3-breed	15%
8-breed	20%
Simplified 3-breed	16%

[1] After Gregory and Cundiff (1980), Baker (1982) and Clarke (1984).

(1979). However, the beef cattle producer in the range environment is rarely able to implement one of the more complicated systems. I believe that, when we describe crossbreeding systems to the range beef cattle producer, we need to emphasize the fact that there are less complicated systems that do a relatively good job of maintaining heterosis. For example, Clarke (1984) has shown that by simply changing the breed of sire every 2 to 4 years, a producer can maintain up to a 16% advantage. This procedure compares very well to some of the more complicated procedures and to synthetics and could be implemented by most range beef cattle producers.

The Dominance Model for Heterosis

It is important to develop a model for heterosis because models: (1) provide a framework within which research results may be discussed and ideas may be expressed; (2) provide the basis or framework from which the predictions may be made (this, of course, assumes that the model is correct); and (3) are useful aids in experimental design because areas that require more research can be identified.

The dominance model, as introduced by Falconer (1960) and others and further developed by Dickerson (1969), will be discussed here because, as Cunningham (1982a) has pointed out, the dominance model has generally done a reasonable job of explaining results from crossbreeding experiments. There are, however, other models that may be more appropriate for certain traits in certain species as discussed by Cunningham (1982a).

Falconer (1981) illustrated the dominance model in a manner similar to that shown in figure 1. The model is illustrated for the single locus with two alleles. Genotypic values expressed as deviations are $-a$ for the A_2A_2 genotype, $+a$ for the A_1A_1 genotype and d for the heterozygote. The measure of the additive effect is a, and d measures the amount of dominance. If a trait were completely determined by the A locus, the frequency of the A_1

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allele was 1 in breed A and the frequency of the A_2 allele was 1 in breed B, then the amount of heterosis in the cross of breed A with breed B would be d. However, allelic frequencies are usually not limited to 0 or 1 so the amount of heterosis must be expressed as a function of the allelic frequencies. If the difference in allelic frequencies between the two parental breeds is expressed as y, then heterosis in the F_1 for one locus is $H_{F1} = dy^2$. If one assumes that effects from different loci combine in an additive manner, then for traits that are determined by n loci, the amount of heterosis in the F_1 can be expressed as:

$$H_{F1} = \sum_{i=1}^{n} d_i y^2 \qquad (1)$$

We may conclude, therefore, that in order for heterosis to be observed there needs to be directional dominance and a difference in gene frequency between the parental breeds. Based on this simple dominance model, the following expectations for performance of the F_1, F_2 and backcrosses may be written as:

$F_1 = P + H_{F1}$

$F_2 = 1/2(P+F_1)$

$B_1 = 1/2(P_1+F_1)$

$B_2 = 1/2(P_2+F_1)$

where P_1, P_2 and P are parental breed 1, parental breed 2 and midparent average, respectively.

These expectations are accurate if there is: (1) no epistatic interaction among the different loci that determine the trait under consideration; (2) a linear relationship between the amount of heterosis and heterozygosity; and (3) no maternal effects for the trait under consideration. It is obvious that for many traits in mammals there are important maternal effects; but for the sake of illustration, we will assume for the moment that they are unimportant.

If one assumes the dominance model, then a schematic design as shown in figure 2 can be drawn to depict the expected performance of inbred lines, purebreds, line crosses and breed crosses. Furthermore, if one considers different levels of crossing, say between Hereford and Simmental, then graphs like those depicted in figure 3 may be constructed to depict the performance of the different possible breed groups when there is no heterosis exhibited by the trait and when there are different types of heterosis exhibited by the trait under consideration. Note that the relationship between performance and proportion of Simmental (degree of heterozygosity) is linear for the three breed groups of HH, 1S3H and 1S1H, regardless of whether heterosis is present or not.

It is obvious that maternal effects could distort the simple diagrams shown in figure 3. For example, figure 4 illustrates performance of the same

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breed groups when there are different types of maternal effects and no heterosis (individual or maternal). Parts (A) and (B) would appear to represent positive and negative heterosis, respectively, when in fact there is no heterosis. Maternal effects could also produce an apparent nonlinear relationship between performance and level of heterozygosity as shown in parts (C) and (D) or produce a situation where a backcross performs below expectation. Therefore, the model must be expanded to take into account other known or expected genetic components such as maternal effects, paternal effects and recombination loss as shown by Dickerson (1969; 1973). The genetic components are as follows:

g_M^I = additive individual effect,

g_A^M = additive maternal effect,

g_A^P = additive paternal effect,
     for breed A,

h_{AB}^I = additive effect,

h_{AB}^M = maternal heterosis,

h_{AB}^P = paternal heterosis,
     for AB and BA F_1 cross,

r_{AB}^I = individual recombination loss,

r_{AB}^M = maternal recombination loss,

r_{AB}^P = paternal recombination loss,
     for AB and BA cross.

The genetic components can be defined as deviations from the mean of n specified purebreds (Dickerson, 1969) or another appropriate base point such as midparent average when considering only two breeds. However, heterosis components should always be expressed as deviations from midparent average. These genetic components can be used to depict performance of different breeds and breed crosses as shown below where the sire breed or breed group is listed first and the dam breed or breed group is listed second:

$$AA = g_A^I + g_A^M + g_A^P,$$

$$AB = 1/2g_A^I + 1/2g_B^I + g_B^M + g_A^P + h_{AB}^I,$$

$$BA = 1/2g_A^I + 1/2g_B^I + g_A^M + g_B^P + h_{AB}^I,$$

$$AxAB = 3/4g^I_A + 1/4g^I_B + 1/2g^M_A + 1/2g^M_B + g^P_A + 1/2h^I_{AB} + h^M_{AB} + 1/4r^I_{AB} \, ,$$

$$AB \times B = 1/4g^I_A + 3/4g^I_B + g^M_B + 1/2g^P_A + 1/2g^P_B + 1/2h^I_{AB} + h^P_{AB} + 1/4r^I_{AB}, \text{ and}$$

$$ABxAB = 1/2g^I_A + 1/2g^I_B + 1/2g^M_A + 1/2g^M_B + 1/2g^P_A + 1/2g^P_B + 1/2h^I_{AB} + h^M_{AB} + h^P_{AB} + 1/2r^I_{AB} \, .$$

The coefficient for r^I is the proportion of independently segregating pairs of loci in the gametes from both parental types which are nonparental (or nonpurebred; e.g., A or B) combinations (Dickerson, 1973). Other genetic components could be (and perhaps should be) included such as the maternal carryover effect ($g^{M'}_A$, $h^{M'}_{AB}$ and $r^{M'}_{AB}$; Dickerson, 1969). Koch et al. (1984) have eloquently reconciled the terminology of Dickerson (1969; 1973), Kinghorn (1980; 1983) and Hill (1982).

The usefulness of a model such as the dominance model is readily apparent. These expectations should be examined when experiments are being designed to determine whether designed comparisons are unbiased estimates of the desired genetic components. In addition, once the genetic components are known, these equations can be used to predict the performance of animals from different kinds of matings in different types of crossbreeding systems (Dickerson, 1974, such as comparing AB vs BA or AxAB vs ABxB.

However, this method of expressing the performance of different breed crosses also raises several questions: Are there interactions among the different components? Do the genetic components interact with the environment? They might change from the more extensive conditions of the western range area to the more intensive management systems observed in other parts of the country. How important are the paternal effects? Does recombination loss depend on history of selection?

Given the possible limitations or over-simplification of the dominance model, it is still a very useful framework within which to work. As an example, consider figure 5 as presented by Dickerson (1973). Purebreds A and C have the same level of performance, but for different reasons. A has a higher mean frequency of favored alleles while C has a higher level of heterozygosity. Purebred B has the highest level of performance because of a high level of heterozygosity and a high mean frequency of favored alleles. Crosses involving breed A would be expected to exhibit more heterosis because breed A is more highly inbred. The cross between breed B and breed C would be expected to exhibit a lower level of heterosis because both of these breeds are already at a relatively higher level of heterozygosity.

Experimental Results from NARC

A crossbreeding experiment was initiated in 1975 at the Northern Agricultural Research Center (NARC) near Havre, Montana. Table 2 shows the design of the experiment and the symbols used to describe the resulting calf breed groups. The first four calf breed groups were all produced from Hereford dams and were raised as contemporaries at the Research Center

TABLE 2. DESIGN AND SYMBOLS

Sire breed	Dam breed	Calf breed
Hereford	Hereford	HH
Angus	Hereford	AH
Simmental x Hereford	Hereford	1S3H
Simmental	Hereford	1S1H
Simmental	Simmental x Hereford	3S1H[a]

[a] Purchased at 10 months of age.

during the years 1976 to 1979. The fifth breed group was produced from Simmental x Hereford dams and was not raised at the Research Center. These heifers were purchased at about 10 months of age from various breeders in the state of Montana. Nine or ten different sires were used to produce each breed group of calf. Further details regarding design, management, sires, and breeding have been given by Lawler et al. (1984) and Kress et al. (1984d). The summer range is located on the northwestern slopes of the Bearpaw Mountains at 1200 m above sea level in northcentral Montana. The vegetation of the site is a rough fescue (Festuca scabrella), Idaho fescue (Festuca idahoensis), bluebunch wheatgrass (Agropyron spicatum) dominated grassland with interspersed areas of pondersosa pine (Pinus ponderosa) overstory. Average annual precipitation is 45 cm. The terrain varies from level to slopes of extreme steepness.

Lawler et al. (1984) demonstrated a breed group difference in calf preweaning growth rate among the first four calf breed groups. The cows that produced these four calf breed groups were Herefords and were managed alike in every controllable way. As a result, we questioned whether the different calf breed groups stressed their dams differentially. Several dam traits were analyzed to determine if calf breed group had a significant effect upon the dam traits. Calf breed group affected ($P < .05$) weight change from precalving to weaning, weight change from precalving to weaning divided by height, condition score at weaning and pregnancy rate. Table 3 shows the pregnancy rate of the Hereford cows was influenced by the calf breed group that the cow raised that summer. Hereford cows raising Hereford calves had a 97% pregnancy rate, while those cows that raised crossbred calves that grew at a faster rate had lower pregnancy rates. This had a large effect on productivity per cow (Kress et al., 1984d). Apparently, the cows were in a borderline feed resource situation and the added stress resulting from faster gaining calves pushed a portion of the cows over the pregnant:nonpregnant threshold. This is an example of an effect that might be seen in a range environment where the forage resource is limited, but may not be seen in other environments where the forage resource is not limiting. Relative to the genetic components discussed earlier, these results suggest an interaction among the components.

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TABLE 3. PREGNANCY RATE FOR HEREFORD COWS RAISING DIFFERENT BREED GROUPS OF CALVES

Calf breed group	Cow pregnancy rate (%)
HH	97
AH	89
1S3H	91
1S1H	82

Table 4 shows the number of heifers that were exposed to breeding as yearlings for each of the five breed groups. The reproductive and maternal abilities of these females through their first calf crop has been summarized by Kress et al. (1984a, b, c). For the purpose of estimating maternal heterosis and determining whether the data support the dominance model, only the four breed groups with different levels of Hereford and Simmental breeding were used.

TABLE 4. NUMBER OF HEIFERS EXPOSED TO BREEDING AS YEARLINGS

Breed group	Number
HH	65
AH	43
1S3H	59
1S1H	45
3S1H	52
Total	264

The genetic components that contribute to the maternal performance (e.g., calf weaning weight) of the four breed groups of cows that vary in amount of Hereford (H) and Simmental (S) breeding when raising Charolais (C) calves are:

$$HH = 1/2g_C^I + 1/2g_H^I + h_{CH}^I + g_H^M + g_H^{M'} + g_C^P \, ,$$

$$1S3H = 1/2g_C^I + 3/8g_H^I + 1/8g_S^I + 3/4h_{CH}^I + 1/4h_{CS}^I + 3/4g_H^M + 1/4g_S^M + 1/2h_{HS}^M$$
$$+ g_H^{M'} + g_C^P + 3/16r_{HS}^I + 1/4r_{HS}^P,$$

$$1S1H = 1/2g_C^I + 1/4g_H^I + 1/4g_S^I + 1/2h_{CH}^I + 1/2h_{CS}^I + 1/2g_H^M + 1/2g_S^M + h_{HS}^M + g_H^{M'}$$
$$+ g_C^P + 1/4r_{HS}^I \text{ and}$$

$$3S1H = \tfrac{1}{2}g^I_C + \tfrac{1}{8}g^I_H + \tfrac{3}{8}g^I_S + \tfrac{1}{4}h^I_{CH} + \tfrac{3}{4}h^I_{CS} + \tfrac{1}{4}g^M_H + \tfrac{3}{4}g^M_S + \tfrac{1}{2}h^M_{HS}$$

$$+ \tfrac{1}{2}g^{M'}_H + \tfrac{1}{2}g^{M'}_S + h^{M'}_{HS} + g^P_C + \tfrac{3}{16}r^I_{HS} + \tfrac{1}{4}r^M_{HS}.$$

The linear contrast of $(2)(1S1H) - 1S3H - 3S1H$ yields an estimate of maternal heterosis as follows:

$$h^M_{HS} + \tfrac{1}{2}g^{M'}_h - \tfrac{1}{2}g^{M'}_S - h^{M'}_{HS} + \tfrac{1}{8}r^I_{HS} - \tfrac{1}{4}r^M_{HS} - \tfrac{1}{4}r^P_{HS}.$$

Thus, maternal carryover maternal effects (M') and(or) effects of recombination loss could bias the estimate of maternal heterosis.

Figures 3 and 4 illustrate that there is a linear relationship between heterosis and the amount of heterozygosity if the dominance model is correct and if there is no recombination loss. There is a linear regression of breed group performance on proportion of Simmental breeding for the three breed groups of HH, 1S3H and 1S1H. This regression was calculated for various traits and the size of the R^2 value was used to evaluate whether or not the data supported the dominance model.

Table 5 gives the R^2 values and the estimates of maternal heterosis for various traits of 2-yr-old dams. Estimates of maternal heterosis for calf growth traits were approximately 8%, ranged from 4 to 27% for calf milk consumption depending upon stage of lactation, ranged from 22 to 41% for reproductive traits and was 32% for calf productivity per yearling heifer exposed to breeding. These large estimates of maternal heterosis strongly support the use of crossbred cows under range conditions. It might be hypothesized that larger estimates of heterosis tend to be found for traits that are composed of several threshold traits. That is, to wean a calf, a heifer must reach puberty by a certain date, must conceive, must give birth to a live calf and the calf must survive to weaning. In addition, all of the R^2 values were high indicating that the dominance model explained the observed results very well.

TABLE 5. R^2 VALUES AND MATERNAL HETEROSIS FOR 2-YR-OLD DAMS

Trait	R^2	Percent
Calf birth weight	.99	7.2
Calf weaning weight	1.00	8.7
Calf milk consumption, early	.99	4.4
Calf milk consumption, late	1.00	26.8
Yearling pregnancy rate	.99	40.7
Proportion calves weaned	.99	22.2
Productivity per heifer exposed	1.00	32.3

Figure 6 shows the cow weights for each breed group of cow during lactation and the calf average daily gain for each breed group of cow. These were 4- and 5-yr-old cows and all were raising calves. The number of cows and

calves for each breed group was 15 or 16, but for some weights, especially from day 84 to 112, the number of cows and calves contributing to the weight was smaller because weights were not taken on a regular basis during the breeding season. In general, the weight pattern of the cows and calf gains followed the range condition very closely. However, some breed groups responded to changes in range condition differently than other breed groups. For example, starting at about day 70 there was ample forage of good quality available to each cow. During this period, the straightbred Hereford cows and the Angus-Hereford cows gained less weight than the crossbred cow groups that contained portions of Simmental breeding. In addition, toward the end of lactation when the quantity and quality of forage was reduced the 75%- and 50%-Simmental cows lost weight while the other cow breed groups tended to gain. The calf average daily gains showed less interaction with the change in range condition. However, the calf average daily gains definitely indicated their dependence on the quantity and quality of range forage and would suggest that under range conditions calf average daily gain from birth to weaning is not a constant value. Thus, different cow breed groups responded differentially to changes in range condition; and calf growth rate near weaning was nonlinear.

Speculation

Most of what follows is based on research results which have lead me to speculate about breeding methods for the range environment. The majority of this section is based on the idea that breed group comparisons, level of heterosis and performance of a given crossbred might interact with environment. These interactions are most likely to be expressed when one of the environments is a rather extensive range environment. Figure 7 introduces this concept. One possible effect of a change in environment is that it might change the slope of the line relating performance and level of heterozygosity. Another possibility is that the relationship might actually be linear in some environments and nonlinear in other environments. This could be caused by desirable epistatic combinations of genes being built up in a particular environment. In that particular environment, the relationship of performance to heterozygosity might be nonlinear due to the epistatic combinations. However, in a different environment, the epistatic combinations may no longer be desirable and the relationship between performance and heterozygosity might actually be linear.

Hearnshaw and Barlow (1982) compared the maternal performance of different F_1 crosses with the straightbred Hereford in high, medium and low environments. Figure 8 summarizes their results for weight of calf weaned per cow bred. In all environments, the straightbred Hereford cow had the poorest performance. However, the breed group that performed the best was different for each environment. In addition, the greatest advantage from crossbred cows was observed in the poorest environment. The authors stated that "at all stages of production, a genetic by environmental interaction occurred. The poorer the environment, the larger the advantage of crossbreeding". Fredeen et al. (1982) reported a location x breed group of dam interaction for calf preweaning growth rate. At Brandon, the breed group of dam ranking was Charolais x Shorthorn (1) > Charolais x Angus (2) > Charolais x Hereford (3) compared to the ranking 3>1>2 at Manyberries. Hence, we should expect

breed group comparisons will change with environment (different ranges or same range at different times of the year as observed in NARC data), especially for reproductive and maternal characteristics and, that as we report, we need to very carefully define the environment in which the research results were generated.

We should expect estimates of heterosis that have been generated in the range environment to be different from those estimates of heterosis that come from other types of environments, especially estimates for reproductive and maternal traits. Table 6 summarizes some results from Wiltbank et al. (1969) that show the dependence of heterosis on the environment for age at puberty in beef heifers. The straightbreds were Hereford and Angus heifers and the crossbreds were the reciprocal crosses of Hereford and Angus. In the high-level environment, there was no heterosis; whereas in the low-level environment, the amount of heterosis was 148 days or 26%. The work of Hohenboken et al. (1976) has shown that level of heterosis in sheep was higher in the more stressful environment for production per ewe. Further evidence for the interaction of heterosis and environment has been examined by Barlow (1981). He concluded that interaction between heterosis and environment is the expectation rather than the exception. Cunningham (1982a) proposed a model to explain differential heterosis in two different environments. He hypothesized that below a certain threshold of environmental severity, the performance of both parental strains may be very poor while the F_1 may show a considerable amount of heterosis. However, in a better environment, one of the strains (in this case, the exotic) may have the genetic potential to perform considerably better and, as a result, the amount of heterosis that is observed may be less. Land (1978) speculated that "apparent" heterosis might result from the atypical performance of a parental breed in a particular environment (i.e., not adapted), which would agree with Cunningham's (1982a) model.

TABLE 6. DEPENDENCE OF HETEROSIS ON ENVIRONMENT FOR AGE AT PUBERTY (DAYS)

Feed level	Straightbred	Crossbred	Heterosis
High	381	381	0
Low	572	424	148

Wiltbank et al. (1969).

One might logically conclude from equation 1 that one way to maximize heterosis is to maximize the difference in gene frequency between the two parental straits. However, an experiment by Moll et al. (1965) with corn indicated that there was a nonlinear relationship between amount of heterosis and the width of the cross and showed that maximum heterosis was exhibited with intermediate widths of crosses while lower levels of heterosis were exhibited when width of cross was small or very wide. This makes sense biologically because in situations where there are wide differences in gene frequencies at many loci, the dominance model may no longer hold. It may be

that the parental strains are so different genetically (and adapted to widely different environments) that they no longer compliment each other and that we should not expect a large degree of heterosis from wide crosses.

Previous paragraphs have suggested an interaction of heterosis with environment and with genotype (width of cross), but perhaps it is really a three-way interaction involving heterosis, environment and genotype as suggested by figure 9. This figure is schematic, but it may serve as a useful model. The horizontal axis has been labeled "Annual Range Production" since we are discussing range cattle here but could just as well have been labeled "Level of Environment" to make it more general. GI, GII and GIII are levels of genotypes. Genotypes within GI would be compatible with other genotypes within GI. The diagram is suggesting that females of GIII are better adapted (or matched) to a range environment with lower annual range production; whereas, females within GI are better adapted to more favorable environments. Matching of maternal genotype to the level of environment is perhaps more important than the matching of the paternal genotype to the environment; and in that sense, there may be some flexibility in the graph in that a mating of GII male by GIII female in a poor environment may be a productive cross. The purpose of the figure is to suggest that the appropriate kinds of crosses to maximize heterosis would be GI by GI in better environment and GIII by GIII in poorer environments. In addition, level of heterosis would be expected to be greater in the poorer environments if the correct paternal and maternal genotypes had been used in the cross. The overall level of productivity would be less in the poorer environments, but the level of heterosis greater. The figure also suggests that the GI by GI mating system would produce little or no heterosis in a poor environment. Thus, heterosis depends not only on the level of environment but, also, on crossing the correct genotypes for that particular environment. This would suggest that the proper order for breeding management by the commercial beef cattle breeder would be to: (1) match the level of management to the environment; (2) match the crossbreeding system to the management and environment; (3) match the type of crossbred female to the crossbreeding system, management and environment; and (4) match the genotype of the sire to the genotype of the dam, crossbreeding system, level of management and environment.

This next point is perhaps more personal opinion than speculation (but please remember that speakers were urged to express personal opinion!). I believe that scientists and producers alike have spent too much time and selection differential (there is an upper limit on both) on development of synthetics. I believe that the way to maximize efficiency of beef production is to use appropriate male and female genotypes in an appropriate crossbreeding system that fits the management and environment. There is merit in studying heterosis retention of F_2's and F_3's but, beyond that, I have difficulty in justifying synthetics. If one takes the point of view used by Falconer (1981) to develop the theory for inbred lines, the situation for synthetics might be similar to that depicted in figure 10. Consider one trait after several strains or breeds are crossed and then allow several sublines to develop from the cross--the expectation is that those sublines would differentiate with time. With no selection taking place over time and if all of those sublines were again crossed, the mean of the

resulting population in a later generation would be equal to the mean of the crossed population at the first generation. As sublines were allowed to develop from this later cross, they would differentiate. If a synthetic or composite was in fact being developed, selection would accompany the process and the trend for the average of all lines would be in an upward direction. However, the generalities of figure 10 should still be true. After the first cross, the average level of heterozygosity in the sublines would gradually decrease. It would eventually decrease to the point that crossing would again be desirable to restore the level of heterozygosity. One can envision this happening over a long period of time if the intent of the breeding program is to develop synthetics. In fact, this is probably what has happened as breeds have developed over time. The second part of figure 10 suggests what probably would happen to overall productivity. After the initial cross, the individual strains or sublines would diverge but most of the sublines would diverge in a downward direction because of loss of heterozygosity. Only the occasional subline would maintain the overall level of performance and this probably would only be maintained by adhering to a strong selection policy. Thus, I believe that for synthetics to maintain their level of productivity a high level of selection must be applied in order to offset the loss in overall productivity due to gradual loss of heterozygosity. I maintain that, on an industry basis, this is wasted selection and that this selection would be more productive if it were practiced on the breeds already in existence. We could then use crossbreeding systems to take advantage of maximum heterosis observed in the F_1 as well as the improved additive genetic merit resulting from selection. As Cunningham (1982b) depicts in the figure on strategic options involving crossbreeding and selection, if heterosis is important and if F_1 production or reciprocal backcrossing is possible, selection should then take place in the parent populations rather than in a gene pool or synthetic. Another reason that I do not favor synthetics for commercial breeders is that there are some paternal and maternal characteristics that tend to be antagonistic--or, using Cartwright's (1982) terminology, "lack of compatibility between Phase I and Phase II". An example discussed in this symposium is the ability of a female to store energy in the form of fat; whereas, that is not normally thought to be a desirable characteristic for a paternal genotype. Crossbreeding systems can take advantage of this antagonism; whereas, synthetics cannot.

Lastly, I would like to summarize areas that I believe deserve further research in the range environment. We need to measure intake and grazing behavior of different breed groups under range conditions. Are some genotypes more adaptable to a variety of range conditions? We need a better understanding of the roles fat deposition and mobilization play in stressful environments. We need estimates of the genetic components in the range environment and we need to determine whether these genetic components interact with each other in order to make accurate predictions. We need experiments to determine the relative importance of paternal genetic components. We frequently assume that the individual heterosis components are equal for different breeds; i.e., $h^I_{AC} = h^I_{AB}$, and this may not be the case. I agree with a conclusion of Cunningham (1982a) that crossbreeding programs should incorporate planned testing of the dominance model.

Conclusions

1. Animal breeders need to improve their descriptions of the range environment in which experimental results are produced.

2. We need to move the lab to the field.

3. There is a continuing need for education in the area of crossbreeding systems.

4. It is important to write out the genetic components for each breed group.

5. Estimates of maternal heterosis for reproductive and maternal traits are large.

6. These results support the dominance model for most traits studied.

7. We need to characterize the genetic components under range conditions.

8. Breed comparisons may depend on the environment.

9. Level of heterosis may depend on the environment.

10. There may be a three-way interaction among heterosis, genotype and environment.

11. Crossbreeding may be more important under range environments.

Literature Cited

Baker, R. L. 1982. The place of crossbreeding in beef cattle improvement. Proc. World Congress on Sheep and Beef Cattle Breeding, New Zealand, Vol. II:General:pp.193-208.

Barlow, R. 1981. Experimental evidence for interaction between heterosis and environments in animals. Anim. Breed. Abstr. 49:715.

Cartwright, T. C. 1982. Objectives in beef cattle improvement. Proc. World Congress on Sheep and Beef Cattle Breeding, New Zealand, Vol. II: General:pp. 19-27.

Clarke, S. E. 1984. Heterosis utilization in the early years of rotational crossbreeding. Proc. West. Sec. Amer. Soc. Anim. Sci. 35:70.

Cundiff, L. V. 1970. Experimental results on crossbreeding cattle for beef production. J. Anim. Sci. 30:694.

Cunningham, E. P. 1982a. The genetic basis of heterosis. 2nd World Congress on Genetics Applied to Livestock Production, Oct. 4-8, Madrid, Spain, Vol. VI:pp. 190-205.

Cunningham, E. P. 1982b. Animal breeding under changing economic circumstances. Proc. World Congress on Sheep and Beef Cattle Breeding, New Zealand, Vol. II:General:pp. 9-17.

Dickerson, G. E. 1969. Experimental approaches in utilizing breed resources. Anim. Breed. Abstr. 37:191.

Dickerson, G. E. 1973. Inbreeding and heterosis in animals. Proc. Anim. Breed. and Gen. Symp. in honor of Dr. J. L. Lush. L. V. Cundiff (Ed.), ASAS and ADSA, Champaign, Illinois, pp. 54-77.

Dickerson, G. E. 1974. Evaluation and utilization of breed differences. Proc. Working Symp. on Breed Evaluation and Crossbreeding Experiments, D. Minkema (Ed.). European Assoc. Anim. Prod., Zeist, Netherland, pp. 7-23.

Falconer, D. S. 1960. Introduction to Quantitative Genetics. The Ronald Press Co., New York.

Falconer, D. S. 1981. Introduction to Quantitative Genetics (2nd Ed.). Longman, New York.

Fredeen, H. T., G. M. Weiss, G. W. Rahnefeld, J. E. Lawson and J. A. Newman. 1982. Environmental and genetic effects on preweaning performance of calves from first-cross cows. II. Growth traits. Can. J. Anim. Sci. 62:51.

Gregory, K. E. and L. V. Cundiff. 1980. Crossbreeding in beef cattle: evaluation of systems. J. Anim. Sci. 51:1224.

Hearnshaw, H. and R. Barlow. 1982. Genotype x environment interactions in crosses among beef cattle. Proc. World Congress on Sheep and Beef Cattle Breeding, New Zealand, Vol. I:Technical:pp.469-474.

Hill, W. G. 1982. Dominance and epistasis as components of heterosis. Z. Tierz. Zuchtungsbiol. 99:161.

Hohenboken, W. D., K. Corum and R. Bogart. 1976. Genetic, environmental and interaction effects in sheep. I. Reproduction and lamb production per ewe. J. Anim. Sci. 42:299.

Kinghorn, B. 1980. The expression of "recombination loss" in quantitative traits. Z. Tierz. Zuchtungsbiol. 97:138.

Kinghorn, B. 1983. Genetic effects in crossbreeding. III. Epistatic loss in crossbred mice. Z. Tierz. Zuchtungsbiol. 100:209.

Koch, R. M., G. E. Dickerson, L. V. Cundiff and K. E. Gregory. 1984. Heterosis retained in advanced generations of crosses among Angus and Hereford cattle. J. Anim. Sci. (Submitted).

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Kress, D. D., D. E. Doornbos, D. C. Anderson and D. D. Trowbridge. 1984a. Productivity of two-year-old straightbred and crossbred dams. I. Calf performance. Proc. West. Sec. Amer. Soc. Anim. Sci. 35:86.

Kress, D. D., D. E. Doornbos, D. C. Anderson and D. D. Trowbridge. 1984b. Productivity of two-year-old straightbred and crossbred dams. II. Dam performance and overall productivity. Proc. West. Sec. Amer. Soc. Anim. Sci. 35:90.

Kress, D. D., D. E. Doornbos and D. C. Anderson. 1984c. Productivity of two-year-old straightbred and crossbred dams. III. Method of estimating heterosis when breed proportions vary and estimates of heterosis. Proc. West. Sec. Amer. Soc. Anim. Sci. 35:94.

Kress, D. D., D. E. Doornbos and D. C. Anderson. 1984d. Performance of crosses among Hereford, Angus and Simmental cattle with different levels of Simmental breeding. II. Effect of calf breed on cow productivity. J. Anim. Sci. 58:1329.

Land, R. B. 1978. Genetic improvement of mammalian fertility: a review of opportunities. Anim. Reprod. Sci. 1:109.

Lawler, T. J., Jr., D. D. Kress, D. E. Doornbos and D. C. Anderson. 1984. Performance of crosses among Hereford, Angus and Simmental cattle with different levels of Simmental breeding. I. Preweaning growth and survival. J. Anim. Sci. 58:1321.

Long, C. R. 1980. Crossbreeding for beef production: experimental results. J. Anim. Sci. 51:1197.

Mason, I. L. 1966. Hybrid vigor in beef cattle. Anim. Breed. Abstr. 34:453.

Moll, R. H., J. H. Lonnquist, J. V. Fortuno and E. C. Johnson. 1965. The relationship of heterosis and genetic divergence in maize. Genetics 52:139.

Notter, D. R., J. O Sanders, G. E. Dickerson, G. M. Smith and T. C. Cartwright. 1979. Simulated efficiency of beef production for a midwestern cow-calf feedlot management system. III. Crossbreeding systems. J. Anim. Sci. 49:92.

Wiltbank, J. N., C. W. Kasson and J. E. Ingalls. 1969. Puberty in crossbred and straightbred beef heifers on two levels of feed. J. Anim. Sci. 29:602.

Genotype	A_2A_2			A_1A_2	A_1A_1
Genotypic Value	$-a$		0	d	$+a$
Arithmetic Value	$\bar{x}-a$		$\bar{x}$	$\bar{x}+d$	$\bar{x}+a$
Genotype Frequency	q^2			$2pq$	p^2
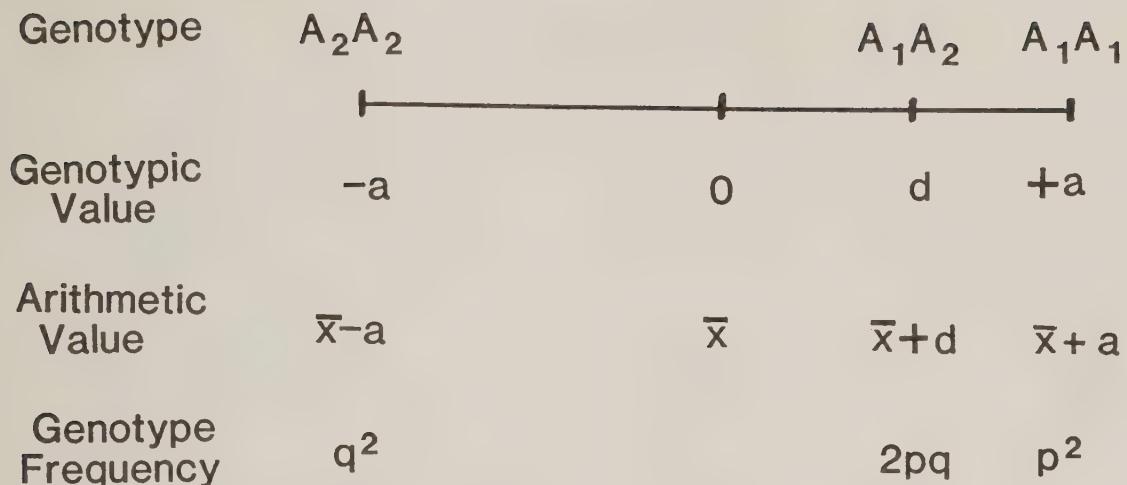
Figure 1. The dominance model for a single locus illustrating the additive genetic effect (a) and dominance (d) (after Falconer, 1981).
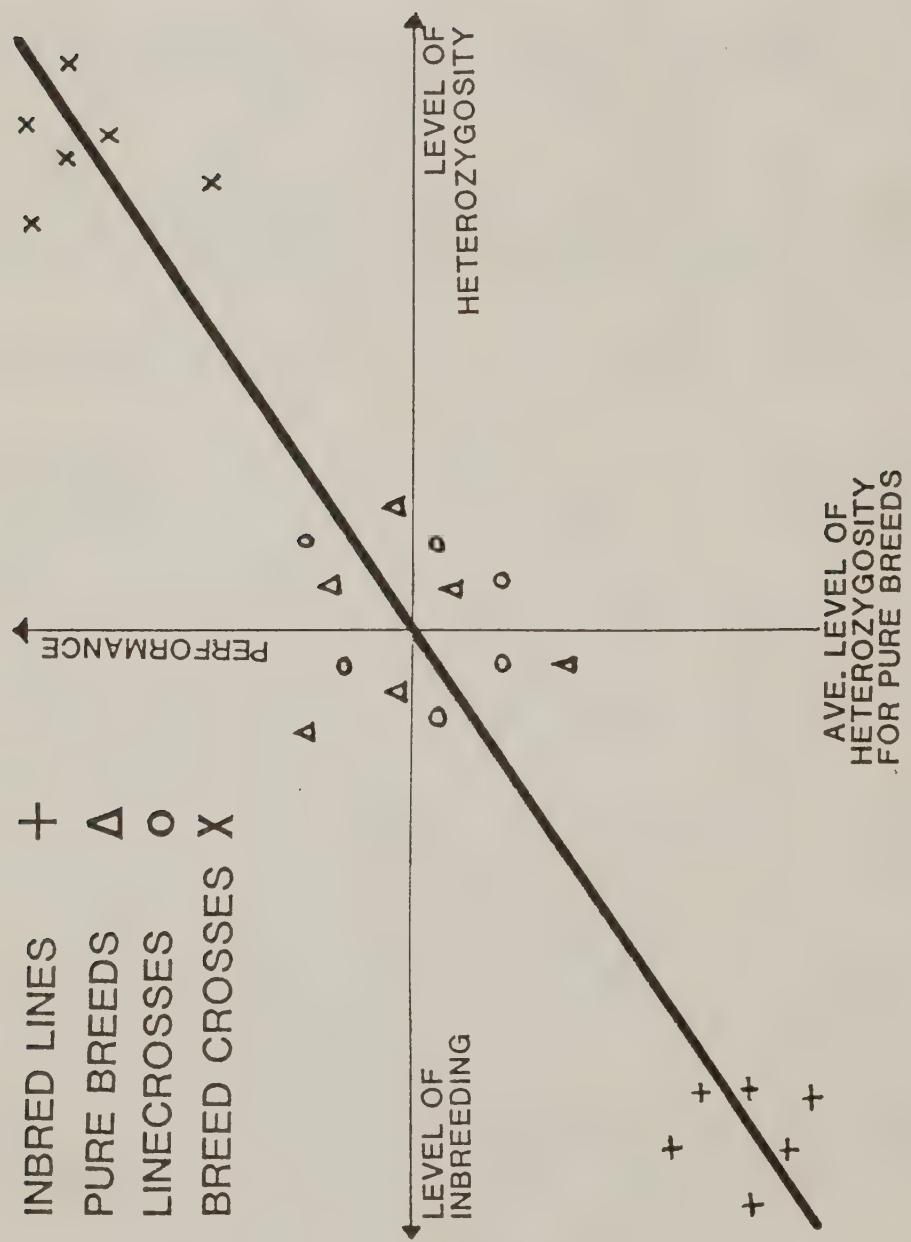
Figure 2. Performance of inbred lines, pure breeds, linecrosses and breed crosses relative to level of heterozygosity (after Dickerson, 1973, and others). Schematic.
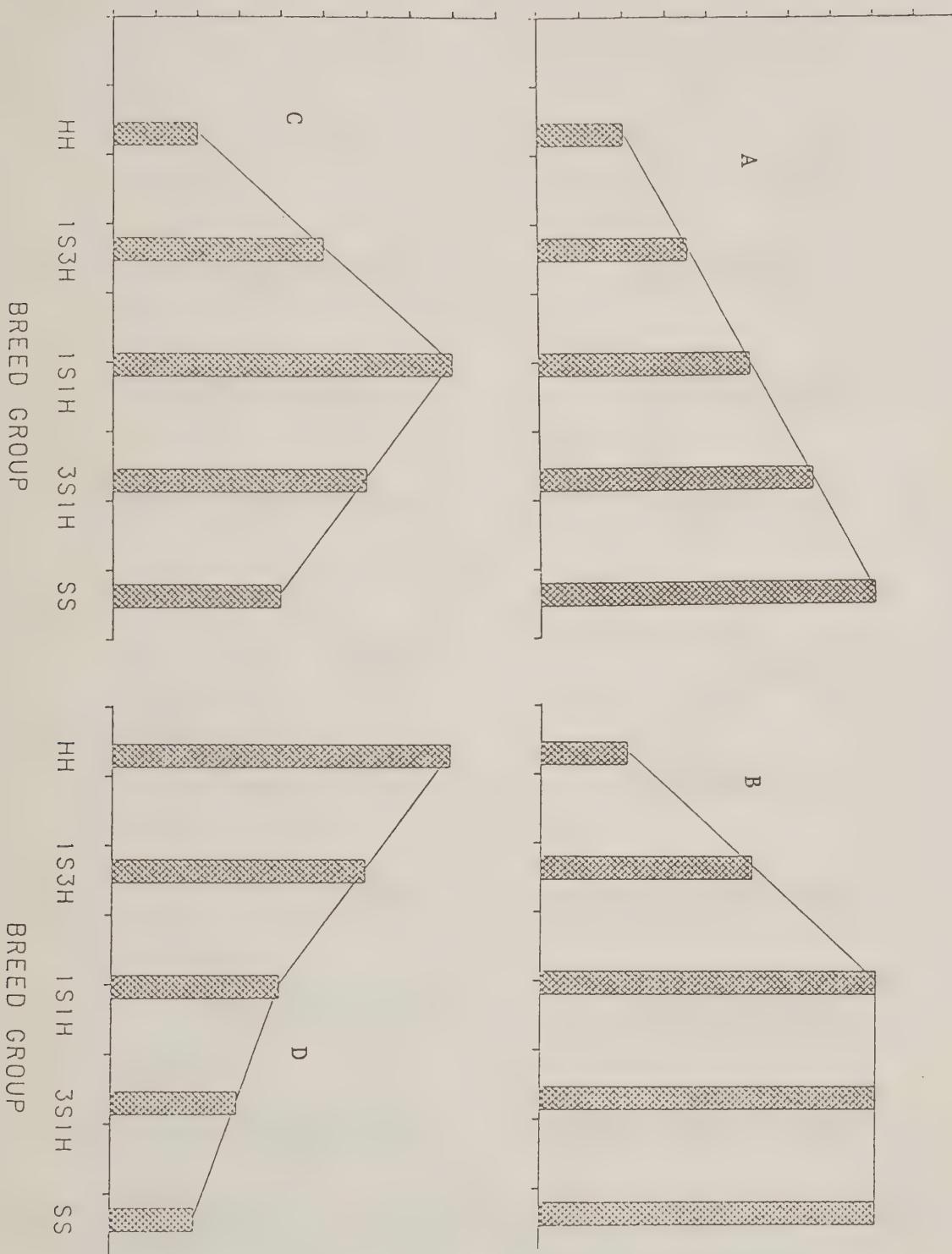
Figure 3. Graphs that depict performance of different breed groups
when there are different levels of heterosis, where HH
= Hereford, 1S3H = 25% Simmental - 75% Hereford, 1S1H =
50% Simmental - 50% Hereford, 3S1H = 75% Simmental - 25%
Hereford and SS = Simmental. (A) No heterosis. (B)
Positive heterosis. (C) Positive heterosis. (D) Negative
heterosis.
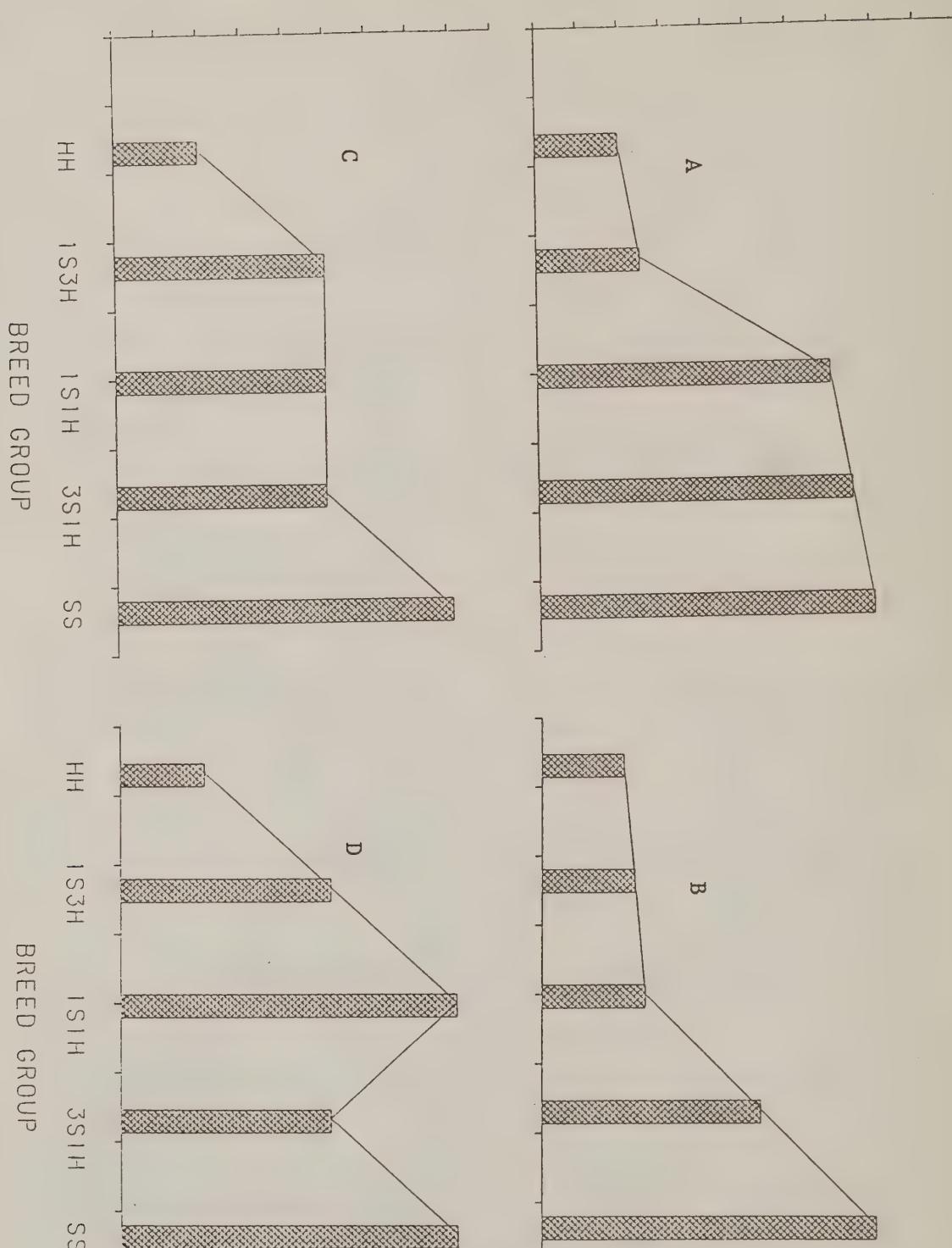
Figure 4. Graphs that depict performance of different breed groups when maternal effects are important (and there is no heterosis), where HH = Hereford, 1S3H = 25% Simmental – 75% Hereford, etc. (A) g_H^T =2, g_H^M =0, g_S^T =4, g_S^M =4 and dam breed groups for respective progeny breed groups = HH, HH, SS, SS and SS. (B) g_H^T = 1, g_H^M = 1, g_S^T = 2, g_S^M = 6 and dam breed groups for respective progeny breed groups = HH, HH, HH, SH and SS. (C) g_H^T = 2, g_H^M = 0, g_S^T=2, g_S^M= 6 and dam breed groups for respective progeny breed groups = HH, SH, SH, SH and SS. (D) g_H^T = 2, g_H^M = 0, g_S^T= 2, g_S^M = 6 and dam breed groups for respective progeny breed groups = HH, SH, SS, SH and SS. See text for definition of genetic components.
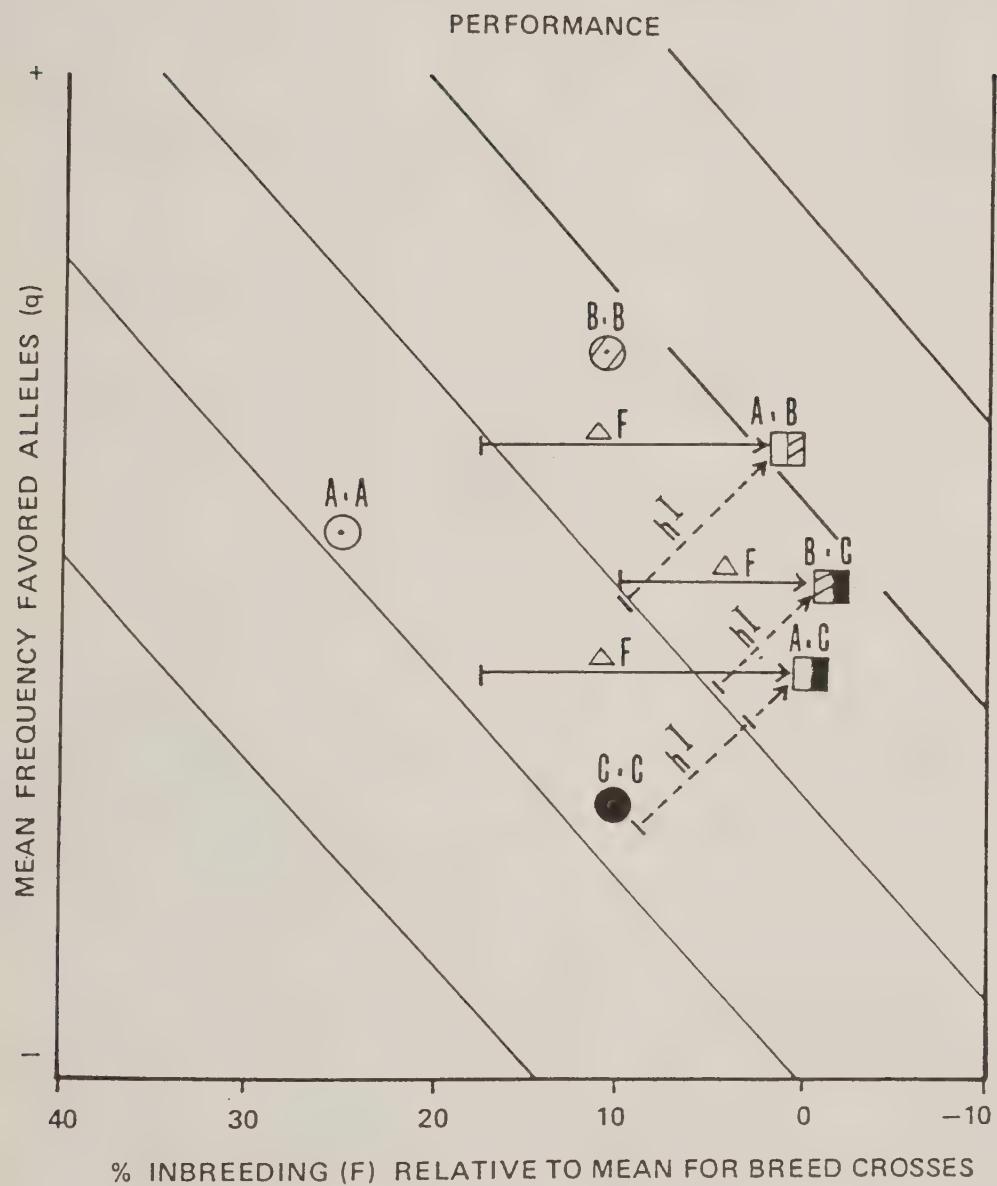
Figure 5. Performance of three breeds (A A, B B and C C) and their crosses (A B, A C and B C) as a function of mean frequency of favored alleles and level of heterozygosity (Dickerson, 1973). Schematic.
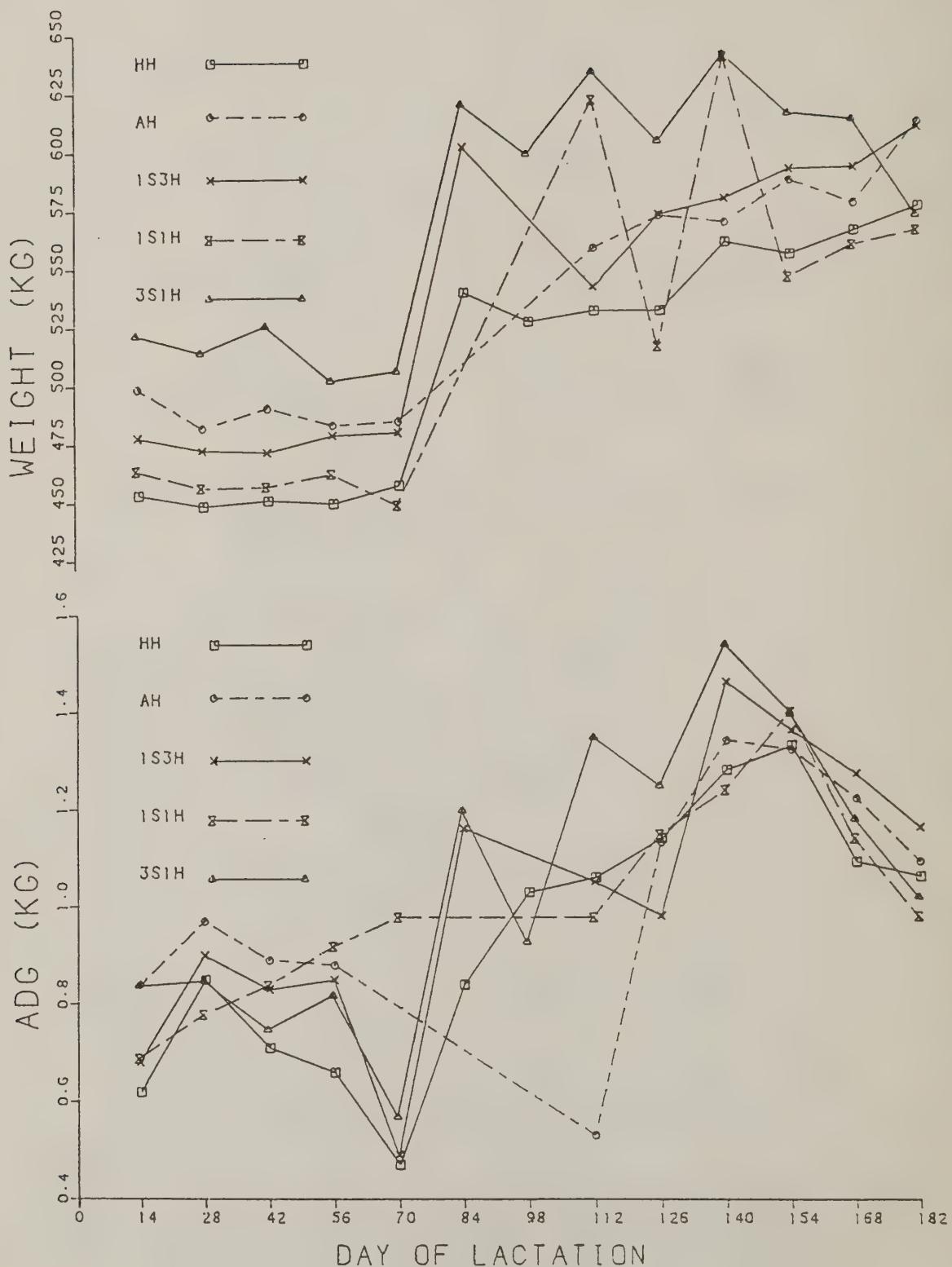
Figure 6. Cow weights and calf average daily gains during
lactation under range conditions.
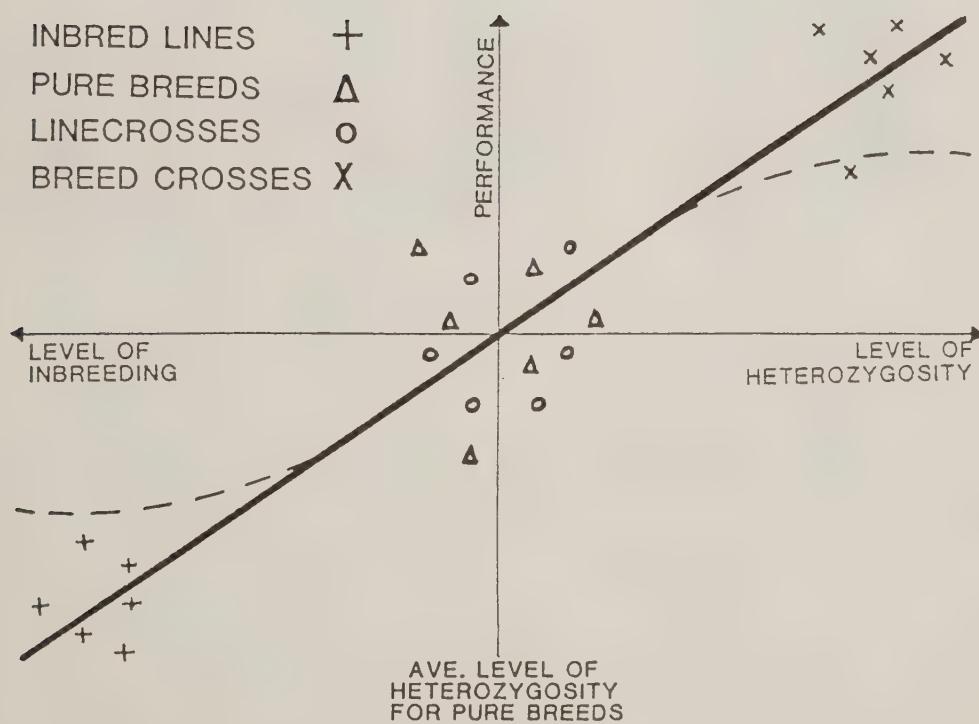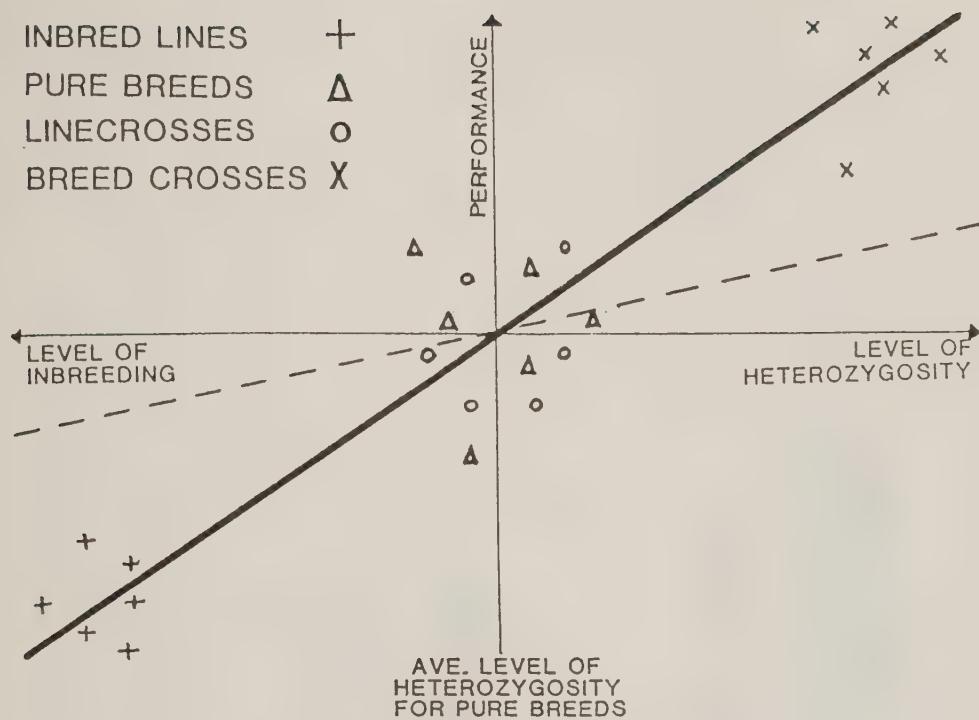
Figure 7.   Possible effect of environment on the performance of
            different genotypes.
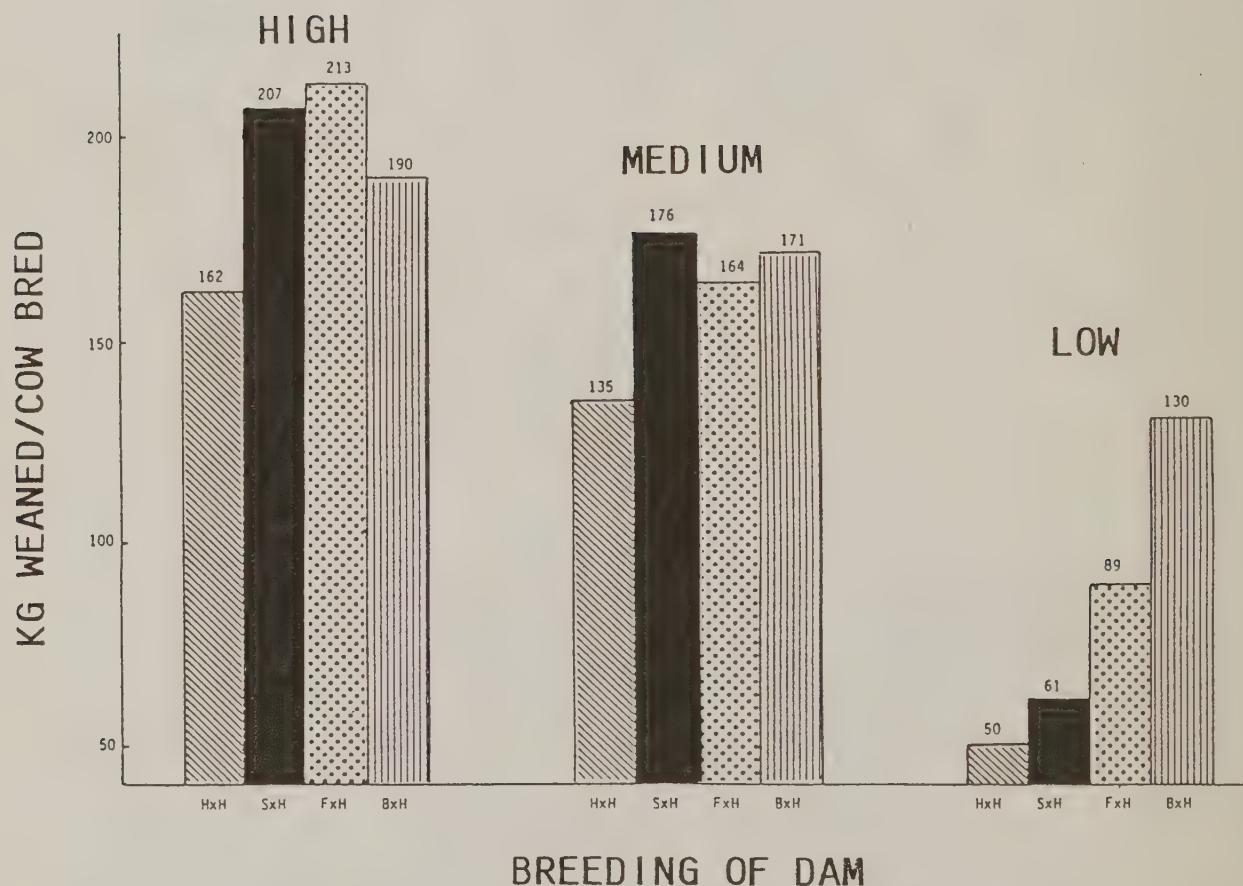
Figure 8. Weight of calf weaned per cow bred for HxH and F_1 cows under high, medium and low nutrition (Hearnshaw and Barlow, 1982).

Figure 9. Interaction of heterosis with environment and genotype. Schematic.
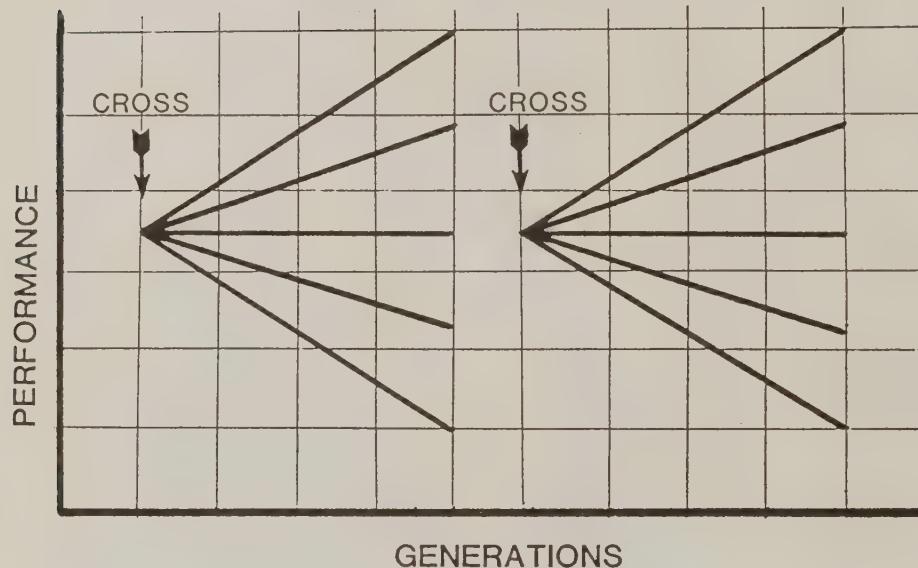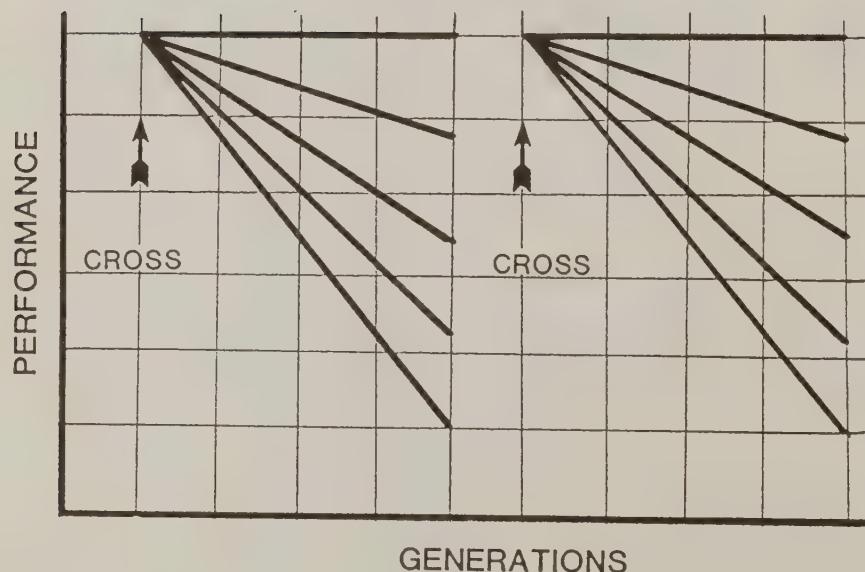
Figure 10. Possible performance of synthetics for one trait and overall performance. Schematic.

GENETICS OF REPRODUCTION IN BEEF CATTLE

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Summary

The effects of individual heterosis from breed crosses on conception rate and early embryo survival are small and likely not important. The effects of individual heterosis are important for calf survival from birth to weaning and vary from 4 to 15%.

The effects of maternal heterosis from breed crosses on conception rate and early embryo survival vary from 6 to 12%. In most experiments, maternal heterosis from breed crosses on calf survival from birth to weaning has been either small or not present. In one experiment, heterosis from breed crosses increased productive life 1.36 years (16.2%). Heterosis to 12 years of age for cow survival (%) was 75.6%, number of calves weaned was 19.8% and calf weight weaned was 29.8% per replacement female. Heterosis observed for age at puberty in females is large (35 to 40 days) and is 13.1 to 17.4% for paired testicular volume in males. Scrotal circumference is an excellent predictor of puberty in males. The effects of individual and maternal heterosis on traits associated with fitness are about twice as great in crosses of Bos indicus breeds with Bos taurus breeds as among crosses of Bos taurus breeds.

Inbreeding effects of calf are greater than inbreeding effects of dam on calf survival; whereas, inbreeding effects of dam are greater than inbreeding effects of calf on conception rate and early embryo survival.

Results from three experiments that permitted estimation of heterosis retained in either rotational crosses or in the F_2 generation from inter se mating indicated that retention of heterosis is approximately proportional to retention of heterozygosity. These results suggest that heterosis observed in breed crosses can be accounted for by dominance effects of genes. Thus, heterosis observed in breed crosses for fitness and other traits can seemingly be accounted for by recovery of accumulated inbreeding depression that has occurred in breeds since their formation. It is likely that much of the inbreeding occurred early in the formation of many of the present breeds of cattle.

Large differences exist among breeds for traits that contribute to fitness. As traits of the calf (additive direct genetic effects), differences among breeds are large for gestation length, birth weight, dystocia, preweaning survival (%), scrotal circumference of males (age at puberty), age at puberty of females and percentage pregnant at 550 days. As traits of the dam (additive maternal genetic effects), differences among breeds are large for calf crop born, calf birth weight, dystocia and preweaning survival (%). Because of the great importance of heterosis and breed effects on fitness traits of major economic importance, high priority is suggested for the development of strategies for the simultaneous use of: (1) differences

among breeds to achieve and maintain near optimum additive genetic (breed) composition and (2) high levels of heterosis.

Estimates of heritability are intermediate to high ($\simeq$ .4) for age at puberty in females and scrotal circumference (age at puberty) in males. The genetic correlation between scrotal circumference in males and age at puberty in females is high (.71). Scrotal circumference in males is favorably associated with libido and desirable semen characteristics. Scrotal circumference should be an effective selection criterion that is favorably associated with several reproduction traits in both sexes. Additional selection criteria to increase reproduction rate (i.e., traits not associated with survival) are not promising.

Dystocia is of major economic importance and seems to be primarily the result of disproportionality in skeletal dimensions of calf and associated skeletal dimensions of dam. Variation in pelvic area regressed on weight adjusted for differences in fat have not been estimated; this information is needed. Differences in skeletal anatomy are highly heritable. This provides a basis for partial solution of the problem if skeletal anatomy can be measured with precision and variation exists in skeletal dimensions of cows and calves.

Large breed differences have been observed in additive maternal genetic effects for uterine environment on prenatal growth. The high genetic correlation between prenatal and postnatal gain of muscle and bone tissue suggests little opportunity to reduce prenatal growth rate as a trait of the calf without a proportional decrease in postnatal growth rate. The opportunity to reduce birth weight and, thus, dystocia by shortening gestation length and(or) by creating a less favorable uterine environment for prenatal growth through selection should be investigated. It is likely that unfavorable biological relationships involving survival may exist between reduced birth weight achieved through either shorter gestation length or a less favorable uterine environment because natural selection would likely favor optimums for both gestation length and uterine environment affecting prenatal growth. It is obvious that genetic/biological factors of calf and of dam that influence dystocia need to be investigated separately and jointly to gain understanding at the level required to manage the problem most effectively.

(Key Words: Reproduction Characters, Heterosis, Inbreeding, Heritability, Genetic Correlations.)

Introduction

The purpose of this paper is to review genetic aspects of reproduction in the context of fitness, i.e., fecundity, postnatal survival and length of productive life. The intent is to present a general overview relating to (1) nonadditive genetic variation, i.e., heterosis and inbreeding effects, (2) additive genetic variation, i.e., average effects of breeds and within breed genetic variation and covariation (heritabilities and genetic correlations).

Results and Discussion

Nonadditive Genetic Variation

Heterosis and Inbreeding. The effects of individual heterosis on prenatal survival are not important but the effects of individual heterosis on survival from birth to weaning are important. Calves alive at weaning were 4% greater in crossbred than in straightbred calves in a diallel experiment involving the Hereford, Angus and Shorthorn breeds (Wiltbank et al., 1967). In a four-breed diallel experiment involving the Angus, Hereford, Red Poll and Brown Swiss breeds, Gregory et al. (1978) reported preweaning survival 3.8% greater in crossbred than in straightbred calves.

Cartwright et al. (1964) reported (table 1) survival to weaning to be 15% greater in crossbred than in straightbred calves involving the Brahman and Hereford breeds; backcross calves did not differ in preweaning survival between crossbred dams with straightbred sires and straightbred dams with crossbred sires (10.4 and 10.6%, respectively), indicating that maternal heterosis on preweaning survival is not important. The apparent negative effects of heterosis on calf crop born in the F_1 generation (-12.2%) were the result of mating preference of Hereford bulls; Hereford bulls were mated to Hereford and Brahman females in the same breeding pasture and showed a preference for mating Hereford females. Cartwright et al. (1964) presented results (table 2) showing maternal heterosis effects on calf crop born of 11.9%; there was not an effect of maternal heterosis on preweaning survival. In a comprehensive experiment involving the Brahman and Shorthorn breeds, Koger et al. (1975) reported the effects of individual heterosis on weaning rate and annual production per cow to be 4.0% and 25.8%, respectively; the effects of maternal heterosis on weaning rate and annual production per cow were 16.6% and 43.5%, respectively.

TABLE 1. EFFECTS OF HETEROSIS ON REPRODUCTION TRAITS OF BRAHMAN-HEREFORD CATTLE[a]

Breed group	Calving (%)		Survival (%)		Weaning (%)	
	Mean (%)	Heterosis (%)	Mean (%)	Heterosis (%)	Mean (%)	Heterosis (%)
Purebred calves	79.6	0	82.4	0	65.9	0
Reciprocal cross calves	69.9	-12.2	94.8	15.0	66.1	0.3
Backcross calves with crossbred dams	87.2	9.5	91.0	10.4	79.3	20.3
Backcross calves with crossbred sires	80.7	1.4	91.1	10.6	73.8	12.0
F_2 calves with F_1 dams	83.0	4.3	89.1	8.1	74.0	12.3

[a] From Cartwright et al. (1964).

TABLE 2. LEAST-SQUARES MEANS REFLECTING HETEROSIS AND BREED EFFECTS ON REPRODUCTION TRAITS[a]

Trait	Dam[b]	Sire[b]			Mean	Heterosis (%)
		H	B	BH		
Calving (%)	H	84.9	76.7	80.1	80.6	
	B	63.0	74.2	81.3	72.8	
	BH	86.6	87.8	83.0	85.8	11.9
	Mean	78.2	79.6	81.5		
Survival (%)	H	88.8	91.1	90.0	90.0	
	B	98.4	75.9	92.1	88.8	
	BH	92.6	89.3	89.1	90.3	1.0
	Mean	93.3	85.4	90.4		
Weaning (%)	H	75.4	69.9	72.3	72.5	
	B	62.3	56.3	75.2	64.6	
	BH	80.1	78.5	74.0	77.5	13.1
	Mean	72.6	68.2	73.8		

[a] From Cartwright et al. (1964).
[b] H = Hereford; B = Brahman.

Cundiff et al. (1974) reported effects of maternal heterosis of 6.6% and 6.4%, respectively, on first-service conception and on calf crop weaned based on cows exposed to breeding involving the Hereford, Angus and Shorthorn breeds in a diallel experiment. In the same females, Wiltbank et al. (1966) reported crossbred females to reach puberty 37 days earlier than the straightbred females. Females were given an opportunity to remain in this experiment to an age of 12 years (Nunez et al., 1984; R. D. Nunez, unpublished data). Heterosis from breed crosses increased productive life 1.36 years (16.2%); heterosis to 12 years of age for cow survival (%) was 75.6%, number of calves weaned was 19.8% and calf weight weaned was 29.8% per replacement female (tables 3 and 4).

TABLE 3. HETEROSIS AND BREED EFFECTS ON LONGEVITY (YEARS) OF HEREFORD, ANGUS, SHORTHORN AND RECIPROCAL CROSS COWS[a]

Breed of dam of cow	Breed of sire of cow			Mean
	Hereford	Angus	Shorthorn	
Hereford	8.46	11.04	9.61	9.70
Angus	10.60	9.41	9.90	9.97
Shorthorn	8.01	9.26	7.28	8.18
Mean	9.02	9.90	8.93	9.28

Heterosis	Crossbred	Straightbred	Difference	
	9.74	8.38	1.36**	(16.2%)

[a] From Nunez et al. (1984).
** P<.01.

TABLE 4. HETEROSIS FOR COW SURVIVAL, CUMULATIVE NUMBER CALVES WEANED AND
CALF WEIGHT WEANED TO 12 YEARS OF AGE FOR HEREFORD, ANGUS AND
SHORTHORN CROSSES[a]

Item	Survival (%)	Number calves weaned	Calf weight weaned (kg)
Purebreds	22.1	5.15	977.8
Crossbreds	38.7	6.17	1268.8
Difference	16.7	1.02	291.1
Heterosis (%)	75.6**	19.8*	29.8**

[a] From R. D. Nunez (unpublished data).
* P<.05; ** P<.01.

Lunstra et al. (1984) reported effects of heterosis on paired testicular
volume to vary from 13.1% to 17.4%. Lunstra et al. (1978) reported scrotal
circumference to be an excellent predictor of puberty in males (27.9±.2 cm)
involving eight breed groups. A correlation of .98 among breed group means
for scrotal circumference in males with age at puberty in females was
reported by Lunstra (1982).

Based on analyses of results from a series of experiments conducted at dif-
ferent locations, Brinks and Knapp (1975) reported inbreeding of calf and of
dam to have a negative effect on traits associated with fitness, i.e.,
reproduction rate and survival (table 5). Inbreeding effects of calf were
greater than inbreeding effects of dam on calf survival to weaning; whereas,
inbreeding effects of dam were greater than inbreeding effects of calf
(embryo) on conception rate and embryo survival. Interpreting these results
on inbreeding effects of calf and of dam in light of results on individual
and maternal heterosis effects suggests that fitness traits that are
affected most by inbreeding are affected most by heterosis, thus, supporting
the dominance hypothesis for heterosis.

TABLE 5. EFFECTS OF INBREEDING OF CALF AND DAM ON REPRODUCTION TRAITS[a]

Trait	Partial regression Calf	Dam
Open, no./(%)	.1287	.2094
Aborted, no./(%)	.0045	.0081
Dead at birth, no./(%)	.0775	.0255
Death from birth to weaning, no./(%)	.0825	.0734
Weaned, no./(%)	-.1645	-.1070

[a] From Brinks and Knapp (1975).

Results from three comprehensive experiments (Cartwright et al., 1964; Koger
et al., 1975; Gregory and Cundiff, 1980) permitted estimation of heterosis

retained in either rotational crosses or in the F_2 generation from inter se mating (tables 6, 7 and 8) and suggest that retention of heterosis is approximately proportional to retention of heterozygosity indicating that heterosis can be accounted for by dominance effects of genes. Thus, heterosis observed for fitness and other traits can seemingly be accounted for by accumulated inbreeding depression that has occurred in breeds since their formation. Perhaps much of the inbreeding occurred early in the formation of many of our present cattle breeds.

TABLE 6. HETEROSIS FOR PRODUCTION PER COW IN HEREFORD, ANGUS, SHORTHORN ROTATIONAL CROSSES[a]

	Two-breed rotation	Three-breed rotation
	First generation	
Observed (%)	16	24
Expected (%)[b]	19	23
	Second generation	
Observed (%)	24	35
Expected (%)[b]	14	21

[a] From Gregory and Cundiff (1980).
[b] Based on individual and maternal heterosis observed in F_1 and assumes that retention of heterosis is proportional to retention of heterozygosity.

TABLE 7. HETEROSIS IN F_2 GENERATION OF HEREFORD-BRAHMAN CROSSES[a]

	Survival (%)	Birth weight	180-day weight	A.D.G. postweaning
Observed (%)	8.1	2.0	17.6	9.5
Expected (%)[b]	7.5	2.7	17.4	5.5

[a] Adapted from Cartwright et al. (1964).
[b] Based on individual heterosis observed in F_1 and assumes that retention of heterosis is proportional to retention of heterozygosity.

TABLE 8. HETEROSIS FOR PRODUCTION PER COW IN BRAHMAN-SHORTHORN CROSSES[a]

	Breed composition of calf	
	3/8-5/8	7/8-1/8
Observed (%)	52.0	21.0
Expected (%)[b]	33.6	25.0

[a] Adapted from Koger et al. (1975).
[b] Based on individual and maternal heterosis observed in F_1 and assumes that retention of heterosis is proportional to retention of heterozygosity.

Based on results from the experiments reviewed, it is concluded that the effects of individual and maternal heterosis on traits associated with fitness are about twice as great in crosses of Bos indicus breeds with Bos taurus breeds as among crosses among Bos taurus breeds.

Additive Genetic Variation

Breed Effects. Comprehensive efforts have characterized breeds for a series of biological traits that contribute to fitness, i.e., fecundity and survival (Gregory et al., 1982; Cundiff et al., 1984; Lunstra et al., 1984). As traits of the calf (additive direct genetic effects), large differences were observed among breeds for gestation length, birth weight, dystocia, preweaning survival, scrotal circumference of males (age at puberty), age at puberty of females and pregnant (%) at 550 days (tables 9, 10 and 11). As traits of the dam (additive maternal genetic effects), large differences were observed among breeds for calf crop born, calf crop weaned, dystocia and preweaning mortality (table 12). As reflected by differences between reciprocal crosses for birth weight, large breed differences exist in additive maternal genetic effects on uterine environment (table 13).

Heritabilities and Genetic Correlations. Several authors have reported estimates of heritability of and genetic correlations among traits that contribute to fitness, i.e., reproduction rate and survival. Estimates of heritability for scrotal circumference of males and age at puberty of females average about .4 (Brinks, 1983; Lunstra, 1982; Lunstra et al., 1984). Brinks et al. (1978) reported a genetic correlation of -.71 between scrotal circumference in males and age at puberty in females. Abadia et al. (1976) reported estimates of heritability of and genetic correlations among semen characters. Heritability of semen characters were low to intermediate (.05 to .30) and genetic correlations among desirable semen characters were favorable. Brinks (1983) reported favorable genetic correlations for age at puberty of females with other biological traits of economic value including weight increase to yearling age, milk production, early calving as 2-year-olds and with cow productivity at younger ages. MacNeil et al. (1984) reported a small negative genetic correlation between age at puberty and lean-to-fat ratio. For traits associated with conception rate, estimates of heritability (table 14) have been low (Dearborn et al., 1973; MacNeil et al., 1984).

Because of the favorable genetic association between scrotal circumference of males and traits contributing to reproductive efficiency of males and reproduction and production efficiency of females, scrotal circumference should be an effective selection criterion that may be favorably associated with several traits that contribute to reproduction efficiency of both sexes. Additional selection criteria for reproduction traits independent of survival are not evident.

Dystocia. Because dystocia is influenced by several biological factors that have important additive direct genetic and additive maternal genetic components involving breed differences as well as within-breed genetic variation and covariation, it is appropriate to discuss dystocia separately and specifically (tables 9, 12, 13, 14 and 15). Further, dystocia is an

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important character affecting both reproduction rate and fitness for which biological understanding is required to most effectively manage the economic "trade-offs". It is likely that dystocia is one of the more important production problems of the beef cattle industry. In addition to increased management and labor costs, perinatal loss is four times greater in calves when dystocia is experienced (Laster and Gregory, 1973; Smith et al., 1976). Also, conception rate in the subsequent breeding season is reduced in females experiencing dystocia (Laster et al., 1973).

TABLE 9. LEAST-SQUARES BREED GROUP MEANS FOR REPRODUCTION TRAITS[a]

Breed group[b]	Number of animals	Gestation length (days)	Calving[c,d] difficulty (%)	Calf[c,e] crop weaned (%)	Birth[c] weight (kg)	Preweaning mortality (%)
Jersey-X	302	282.9	2.9	92.3	31.1	7.7
Hereford-Angus-X	962	284.0	2.9	97.3	35.7	2.7
Red Poll-X	214	285.2	3.7	97.8	35.7	2.2
South Devon-X	232	286.7	11.9	92.9	37.7	7.1
Tarentaise-X	202	287.1	6.0	94.8	37.5	5.2
Pinzgauer-X	376	286.0	6.3	95.2	39.2	4.8
Sahiwal-X	325	294.0	6.2	94.3	38.0	5.7
Brahman-X	349	291.7	10.0	93.5	40.9	6.5
Brown Swiss-X	263	285.0	8.4	97.2	38.8	2.8
Gelbvieh-X	213	286.3	8.0	91.5	39.0	8.5
Simmental-X	399	287.3	14.9	89.1	40.3	10.9
Maine Anjou-X	222	285.4	20.4	90.8	41.1	9.2
Limousin-X	371	289.2	9.4	91.7	38.9	8.3
Charolais-X	382	287.0	18.4	86.5	41.1	13.5
Chianina-X	238	287.5	11.8	91.1	40.5	8.9
Hereford dams	2440	288.6	10.1	93.0	39.1	7.0
Angus dams	3129	285.4	6.5	94.2	36.7	5.8

[a] From Gregory et al. (1982).
[b] All calves were by breed of sire listed and were out of Hereford and Angus straightbred dams.
[c] Calving difficulty (%), calf crop weaned (%) and birth weight data are from cows calving at 4 years of age or older.
[d] Calving difficulty (%) is percentage of normal presentations requiring calf puller or C-section.
[e] Calf crop weaned is expressed as a percentage of all dams calving.

TABLE 10. LEAST-SQUARES BREED GROUP MEANS FOR REPRODUCTION TRAITS OF FEMALES[a]

Breed group	Number	Weight at puberty (kg)	Weight at puberty ratio[b]	Age at puberty (days)	Age at puberty ratio[b]	Pregnant 550 days (%)
Jersey-X	117	235	83	308	86	80.6
Hereford-Angus-X	322	282	100	357	100	87.2
Red Poll-X	95	263	93	337	94	84.8
South Devon-X	120	290	103	350	98	79.3
Tarentaise-X	85	282	100	349	98	96.2
Pinzgauer-X	114	277	98	334	94	99.2
Sahiwal-X	87	291	103	414	116	103.2[c]
Brahman-X	103	323	114	429	120	98.2
Brown Swiss-X	126	279	99	332	93	93.0
Gelbvieh-X	81	284	101	326	91	93.2
Simmental-X	157	302	107	358	100	80.4
Maine Anjou-X	89	305	108	357	100	94.2
Limousin-X	161	308	109	384	108	76.2
Charolais-X	132	319	113	384	108	74.8
Chianina-X	92	317	112	384	108	85.6
Hereford dams	997	291		379		90.4
Angus dams	1103	288		351		87.7

[a] From Gregory et al. (1982).
[b] Ratio relative to Hereford-Angus crosses.
[c] In Cycle III, only 82.0% of Angus-Hereford crosses were pregnant at 550 days; whereas, 98% of the Sahiwal crosses were pregnant at 550 days.

Dystocia seems to be primarily the result of disproportionality in skeletal dimensions of calf and associated skeletal dimensions of dam. Dystocia has increased because of several changes in the beef cattle industry during the last two decades, i.e., (1) change to 2-year-old calving programs in much of the industry and dystocia is greatest in 2- and 3-year-old females (Smith et al., 1976); (2) increased emphasis on yearling weight selection resulting in heavier birth weight (Koch et al., 1982); and (3) some shift to breeds that have faster growth rate and larger mature size. Skeletal dimensions of adult animals do not increase in proportion to weight, thus, tending to result in more dystocia in breeds with faster growth rate and larger mature size (Menessier, 1976).

TABLE 11. SCROTAL CIRCUMFERENCE, TESTICULAR LENGTH AND PAIRED TESTICULAR VOLUME OF YEARLING MALES[a]

Breed group	SC[b] (mm;SE=±3) 354 days	Mean TL[b] (mm;SE=±1) 354 days	PTV[b] (cm³; SE=±10) 354 days
Limousin	288	95	318
Hereford	301	94	342
Charolais	314	100	401
Angus	319	103	421
Red Poll	323	102	427
Pinzgauer	334	109	488
Simmental	334	111	497
Brown Swiss	335	114	512
Gelbvieh	336	112	509

[a] From Lunstra et al. (1984).
[b] SC = scrotal circumference, TL = average length of both testicles and PTV = paired testicular volume.

TABLE 12. LEAST-SQUARES BREED GROUP MEANS FOR REPRODUCTION TRAITS[a]

Breed group[b]	Number births	Calving difficulty (%)	Calf crop Born (%)	Calf crop Weaned (%)	Preweaning mortality (%)
Jersey-X	628	7	90	84	6.7
Hereford-Angus-X	1685	13	91	84	7.7
Red Poll-X	461	14	90	79	12.2
South Devon-X	603	15	88	85	3.4
Pinzgauer-X	508	13	93	85	8.6
Tarentaise-X	369	10	91	85	6.6
Sahiwal-X	431	2	95	89	6.3
Brahman-X	519	1	94	86	8.5
Simmental-X	872	17	89	83	6.7
Brown Swiss-X	681	8	92	85	7.6
Gelbvieh-X	429	11	95	87	8.4
Maine Anjou-X	468	11	94	86	8.5
Limousin-X	851	12	89	82	7.9
Charolais-X	693	15	88	80	9.1
Chianina-X	475	8	93	86	7.5

[a] From Cundiff et al. (1984).
[b] All cows were by the breed of sire listed and were out of Hereford and Angus straightbred dams in each breed group.

TABLE 13. RECIPROCAL EFFECTS ON REPRODUCTION TRAITS[a]

Contrast[b]	Birth weight (kg)	Gestation length (days)	Calving difficulty (%)	Perinatal mortality (%)	Calf crop weaned (%)
BR–RB	.6	−1.9	19.8**	6.5	.7
HR–RH	1.3	−1.0	7.9	5.4*	−6.3
AR–RA	2.4**	.2	1.7	−1.1	.3
HB–BH	4.0**	2.6**	−12.8*	2.8	−1.9
AB–BA	2.0*	1.8*	−5.4	−1.2	1.1
AH–HA	−.4	.1	−1.6	.0	−1.6

[a] From Gregory et al. (1978).
[b] R = Red Poll, B = Brown Swiss, H = Hereford, A = Angus; sire breed listed first.
* P<.05; ** P<.01.

TABLE 14. HERITABILITY ESTIMATES OF REPRODUCTION TRAITS

Trait	h^{2a}	h^{2b}	h^{2c}
Age at puberty		.61±.12	
Weight at puberty		.70±.11	
Conception/service		.03±.13	
Gestation length		.30±.18	.55±.07
Calving difficulty		.22±.18	.30±.11
Birth weight		.37±.17	.33±.06
Calf survival			.06±.10
First service conception rate	.22±.17		
Conceptions per estrous cycle	.27±.17		

[a] From Dearborn et al. (1973).
[b] From MacNeil et al. (1984) -- considered as traits of dams.
[c] From Cundiff et al. (1982) -- considered as traits of calf.

TABLE 15. GENETIC[a] AND PHENOTYPIC[b] CORRELATIONS AMONG REPRODUCTION TRAITS[c]

Trait	Gestation length	Birth weight	Calving difficulty	Calf survival
Gestation length		.58	.24	−.03
Birth weight	.40		.70	−.61
Calving difficulty	.08	.18		−.56
Calf survival	.01	.01	−.14	

[a] Above diagonal.
[b] Below diagonal.
[c] From Cundiff et al. (1982).

Dystocia seems to be due primarily to disproportionality between skeletal dimensions of dam and of calf and differences in skeletal anatomy are highly heritable. This provides a basis for partial solution to the problem. Even with relatively imprecise methods of measurement, pelvic area is a trait with intermediate to high heritability (Green et al., 1984). It is important to determine if there are major deviations from linearity of pelvic area regressed on live weight adjusted for differences in fat. It has been suggested that shape of skeletal anatomy of dam, including angle of pelvis, may have a major influence on dystocia but adequate documentation of this relationship has not been provided and is needed.

Birth weight has a major influence on dystocia (Laster et al., 1973). As a trait of the calf, there are large differences in dystocia among breed groups with similar birth weight (Gregory et al., 1982) suggesting that differences in skeletal dimensions of calves with the same birth weight contribute to dystocia (table 9). There is likely a high (>.8) genetic correlation between prenatal and postnatal growth rate of muscle and bone tissue (Gregory, 1982). Thus, there seems to be little opportunity to decrease birth weight resulting from additive direct genetic effects without experiencing a corresponding decrease in subsequent growth rate and mature size. Large breed differences have been observed in additive maternal genetic effects as reflected by differences in birth weight between reciprocal crosses (Gregory et al., 1978). Evidence suggests that this large maternal effect on prenatal growth is due to differences in uterine environment rather than to differences in ovum cytoplasm (Maurer et al., 1983). The effects of differences in uterine environment on composition of prenatal gain have not been evaluated. Both additive direct genetic effects (genes of the calf) and additive maternal genetic effects (uterine environment) have major effects on birth weight.

Gestation length influences birth weight (Cundiff et al., 1982b and table 15). As a trait of the calf, Cundiff et al. (1982b) reported a high heritability (.55) for gestation length and, as a trait of the dam, MacNeil et al. (1984) reported a heritability of .30 for gestation length (table 14). The reason for the difference between the two estimates is not apparent; when considered as a trait of the dam, additive direct genetic effects and additive maternal genetic effects are confounded; whereas, when gestation length is considered as a trait of the calf, the estimate is based on additive direct genetic effects. Thus, this difference in estimates suggests the possibility of a negative genetic covariance between additive direct genetic effects and additive maternal genetic effects for gestation length.

Average birth weight of calves of the same breed groups and of similar breeding were 8.2 kg heavier at birth at Clay Center, Nebraska, than at Brooksville, Florida. There is a large climatic effect on prenatal growth rate and dystocia. Results suggest that, even though protein and energy nutrition can influence birth weight, their influence on dystocia is small. Thus, the climatic effect on prenatal growth and dystocia seemingly is through temperature and/or mineral nutrition. At the U.S. Meat Animal Research Center, fall-born calves are lighter at birth and experience less dystocia than spring-born calves. Nutritive environment (protein, energy and mineral) in the last trimester of gestation should be more favorable in cows gestating fall-dropped calves.

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Increased calf survival is a primary objective of reducing dystocia. Increased calf survival suggests optimums for both gestation length and for birth weight (Cundiff et al., 1982a). Dickerson et al. (1974) suggested a selection index for growth that would give a negative value to birth weight (Index = adjusted yearling weight - 3.2 x birth weight) as an approach to increasing postnatal growth rate with less change in birth weight and dystocia. Because of the likely high genetic correlation between prenatal and postnatal growth rate of muscle and bone tissue (additive direct genetic effects), this index would be expected to result in selection pressure for reduced gestation length and/or for less favorable prenatal maternal effects (uterine environment) on prenatal growth. Even though we do not believe that this approach is indicated for industry practice at this time, the matter of understanding genetic variances and covariances involving both additive direct genetic effects and additive maternal genetic effects relating to dystocia and associated biological characters should receive high priority in research efforts.

Bos indicus breeds and relatively high milking Bos taurus breeds that have been maintained under a high level of husbandry seem to represent the extremes in additive maternal genetic effects for prenatal growth rate (uterine environment) (K. E. Gregory, unpublished data). The effects of uterine environment, involving these biological extremes, on composition of prenatal gain is not known. It seems likely that natural selection for fitness is the basis for the evolution of these large differences in uterine environment that influence prenatal growth. Thus, it is likely that these differences in uterine environment that affect prenatal growth relate to survival in the widely divergent climatic and husbandry environments under which Bos indicus and relatively high milking Bos taurus cattle have been maintained.

Literature Cited

Abadia, D., J. S. Brinks and E. J. Carroll. 1976. Genetics of seminal traits in young beef bulls. Proc. West. Sec. Amer. Soc. Anim. Sci. 27:30.

Brinks, J. S. 1983. Genetic aspects of reproduction in beef cattle. 34th Annual Beef Cattle Improvement Report and Sale Data. Special Series 25:18. Colorado State Univ. Exp. Sta., Fort Collins.

Brinks, J. S. and B. W. Knapp. 1975. Effects of inbreeding on performance traits of beef cattle in the Western Region. Tech. Bull. 123. Colorado State Univ. Exp. Sta., Fort Collins.

Brinks, J. S., M. J. McInerney and P. J. Chenoweth. 1978. Relationship of age at puberty in heifers to reproductive traits in young bulls. Proc. West. Sec. Amer. Soc. Anim. Sci. 29:28.

Cartwright, T. C., G. F. Ellis, Jr., W. E. Kruse and E. K. Crouch. 1964. Hybrid vigor in Brahman-Hereford crosses. Tech. Monogr. 1. Texas Agr. Exp. Sta.

Cundiff, L. V., K. E. Gregory and R. M. Koch. 1974. Effects of heterosis
    on reproduction in Hereford, Angus and Shorthorn cattle. J. Anim. Sci.
    38:711.

Cundiff, L. V., K. E. Gregory and R. M. Koch. 1982a. Selection for
    increased survival from birth to weaning. Proc. of 2nd World Congress
    on Genetics Applied to Livestock Production. V:310.

Cundiff, L. V., K. E. Gregory and R. M. Koch. 1984. Cattle germ plasm
    evaluation program progress report. No. 11, ARS-1.

Cundiff, L. V., M. D. MacNeil, K. E. Gregory and R. M. Koch. 1982b.
    Genetic analysis of calving traits and survival to weaning in cattle.
    J. Anim. Sci. 55(Suppl. 1):143.

Dearborn, D. D., R. M. Koch, L. V. Cundiff, K. E. Gregory and G. E.
    Dickerson. 1973. An analysis of reproductive traits in beef cattle.
    J. Anim. Sci. 36:1032.

Dickerson, G. E., N. Kunzi, L. V. Cundiff, R. M. Koch, V. H. Arthaud and
    K. E. Gregory. 1974. Selection criteria for efficient beef produc-
    tion. J. Anim. Sci. 39:659.

Green, R. D., J. S. Brinks, A. H. Denham and D. G. Lefever. 1984. Estima-
    tion of heritabilities of pelvic measures of beef cattle. J. Anim.
    Sci. 59(Suppl. 1):174.

Gregory, K. E. 1982. Breeding and production of beef to optimize produc-
    tion efficiency, retail product percentage and palatability character-
    istics. J. Anim. Sci. 55:716.

Gregory, K. E. and L. V. Cundiff. 1980. Crossbreeding in beef cattle:
    Evaluation of systems. J. Anim. Sci. 51:1224.

Gregory, K. E., L. V. Cundiff and R. M. Koch. 1982. Comparison of
    crossbreeding systems and breeding stocks used in suckling herds of
    continental and temperate areas. Proc. of 2nd World Congress on
    Genetics Applied to Livestock Production. V:482.

Gregory, K. E., L. V. Cundiff, R. M. Koch, D. B. Laster and G. M. Smith.
    1978. Heterosis and breed maternal and transmitted effects in beef
    cattle. I. Preweaning traits. J. Anim. Sci. 47:1031.

Koch, R. M., L. V. Cundiff and K. E. Gregory. 1982. Sixteen years of
    selection for weaning weight, final weight and muscling score in
    Hereford cattle. Beef Research Program Progress Rep. No. 1. ARS,
    USDA. ARM-NC-21.

Koger, M., F. M. Peacock, W. G. Kirk and J. R. Crockett. 1975. Heterosis
    effects on weaning performance of Brahman-Shorthorn calves. J. Anim.
    Sci. 40:826.

Laster, D. B., H. A. Glimp, L. V. Cundiff and K. E. Gregory. 1973. Factors affecting dystocia and effects of dystocia on subsequent reproduction in beef cattle. J. Anim. Sci. 36:695.

Laster, D. B. and K. E. Gregory. 1973. Factors influencing peri- and early postnatal mortality. J. Anim. Sci. 37:1092.

Lunstra, D. D. 1982. Testicular development and onset of puberty in beef bulls. Beef Research Program Progress Report No. 1. ARS, USDA, ARM-NC-21.

Lunstra, D. D., J. J. Ford and S. E. Echternkamp. 1978. Puberty in beef bulls: Hormone concentrations, growth testicular development, sperm production and sexual aggressiveness in beef bulls of different breeds. J. Anim. Sci. 46:1054.

Lunstra, D. D., K. E. Gregory and L. V. Cundiff. 1984. Breed group differences and heritability of testicular development in yearling beef bulls. Proc. 10th Int. Congr. Anim. Reprod. Artific. Insem. III:527.

MacNeil, M. D., L. V. Cundiff, C. A. Dinkel and R. M. Koch. 1984. Genetic correlations among sex-limited traits in beef cattle. J. Anim. Sci. 58:1171.

Maurer, R. R., K. E. Gregory, S. E. Echternkamp, L. V. Cundiff and R. M. Koch. 1983. Progress report on effects of ovum cytoplasm, uterine environment and postnatal environment in contributing to maternal effects in cattle. J. Anim. Sci. 57(Suppl. 1):159.

Menessier, F. 1976. Comments on optimization of cattle breeding schemes: Beef breeds for suckling herds: A review. Ann. Genet. Sel. Anim. 8:71.

Nunez, R. D., L. V. Cundiff, G. E. Dickerson and K. E. Gregory. 1984. Heterosis of longevity in beef cattle. J. Anim. Sci. 59(Suppl. 1):180.

Smith, G. M., D. B. Laster and K. E. Gregory. 1976. Characterization of biological types of cattle. I. Dystocia and preweaning growth. J. Anim. Sci. 43:27.

Wiltbank, J. N., K. E. Gregory, J. A. Rothlisberger, J. E. Ingalls and C. W. Kasson. 1967. Fertility of beef cows bred to produce straightbred and crossbred calves. J. Anim. Sci. 26:1005.

Wiltbank, J. N., K. E. Gregory, L. A. Swiger, J. E. Ingalls, J. A. Rothlisberger and R. M. Koch. 1966. Effects of heterosis on age and weight at puberty in beef heifers. J. Anim. Sci. 25:744.

THE CONCEPT OF PERFORMANCE TESTING

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Since we are in Miles City, home of Fort Keogh Livestock and Range Research Station, it seems appropriate that we begin our discussion of performance testing with a bit of history. Dr. Frank Baker (1984) lists many important dates dealing with the history of beef cattle performance testing in the United States. This list begins with:

> 1930-1935. Genesis of the idea; the first research initiated by USDA at the U. S. Range Livestock Experiment Station, Miles City, Montana.

Baker's list documents many other milestones in the history of the performance testing movement, including the initiation of research programs, extension programs, the formation of state BCIA's and breed association performance and sire evaluation programs. Notable among these important events was the initiation of the Regional Beef Cattle Breeding Projects developed in three regions: Western (W-1), 1946; North Central (NC-1), 1947; and Southern (S-10), 1948. Research results from these projects laid the foundation for performance testing programs that followed. Many performance programs were developed as state extension or BCIA programs. Performance Registry International (PRI) was formed and breed associations, along with several private programs, were developed. A need evolved for some standardization in methods and terminology and the Beef Improvement Federation (BIF) was founded in 1968 to accomplish this task. This Federation of organizations involved in performance testing has been active since that time and has honored many researchers, extension personnel and cattlemen as pioneers in the performance testing movement.

Concept of Performance Testing

Record of performance or performance testing is the systematic measuring and recording of performance or indicators of performance traits. This recorded data becomes a data bank which, upon proper manipulations and analyses, is used in selection and management programs.

The primary objective of performance testing programs is to characterize germ plasm so that superior seedstock can be identified and used to produce future generations. The "superior seedstock" may differ widely depending upon the environment, feed resources or specific purposes for which they will be used. An important spin-off of these programs is the study of environmental effects on performance traits. This information can be valuable in making management and production decisions.

In performance testing programs, we collect and record phenotypic values on many traits. Each animal has a separate phenotypic value for each trait. Each phenotypic value is completely determined by its genotypic value and environmental effects to which the animal has been subjected until time of measurement. This relationship can be depicted as $P = G + E$. Figure 1 depicts a further breakdown of genotypic value and environmental effects.

Figure 1. Values and effects that contribute to phenotypic value of an animal for a specific trait.
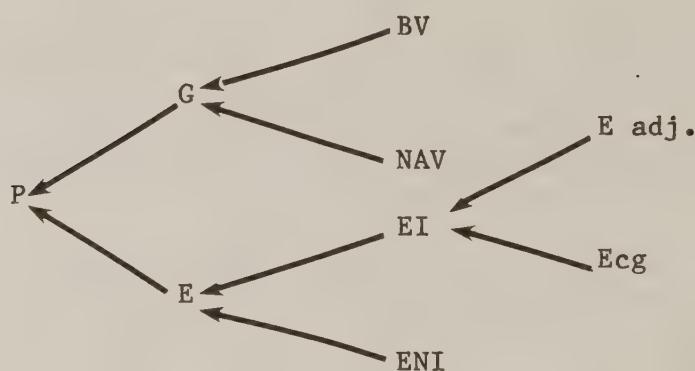
P = Phenotypic value
   G = Genotypic value
      BV = Breeding value
      NAV = Nonadditive value

   E = Environmental effects
      EI = Identifiable environmental effects
      E adj. = Environmental effects for which adjustments are made
      Ecg = Environmental effects associated with contemporary groups
      ENI = Nonidentifiable or random environmental effects

The values in figure 1 can also be written in various forms as:

$$P = G + E \qquad\qquad G = BV + NAV$$
$$P = BV + NAV + EI + ENI \qquad\qquad E = EI + ENI$$
$$P = BV + NAV + E\ adj. + Ecg + ENI \qquad\qquad E = E\ adj. + Ecg + ENI$$
$$EI = E\ adj. + Ecg$$

The genetic value for an animal for a specific trait can be partitioned into two components, the additive or breeding value (BV) and the nonadditive value (NAV). The BV is the worth of an animal as a parent and is determined by what genes an animal possesses that can be passed on to its progeny. Therefore, BV is important in determining response to selection and the whole performance testing concept deals with estimating BV as accurately as possible.

The nonadditive value is determined by the gene combinations an animal has, whether gene combinations are in the homozygous or heterozygous state and nonadditive gene action such as dominance and epistasis. This value is not passed on from parent to offspring since only a sample one-half of an animal's genes are present in the sperm or ovum. This value must be reconstructed each generation using various mating systems such as crossbreeding or inbreeding.

Likewise, environmental effects that influence the phenotypic value can be divided into identifiable and nonidentifiable sources. Identifiable environmental effects can be subdivided into those that we adjust for and

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those associated with differences among contemporary groups. Those identifiable environmental effects that have a relatively consistent effect over animals, such as age of animal, age of dam and sometimes sex of animal, can be used to render an adjusted phenotypic value, P adj. = BV + NAV + Ecg + ENI. Thus, differences among animals due to effects of E adj. have been removed. An example would be the adjusted 205-day weaning weight.

Selections are normally made within contemporary groups--groups of animals born in the same year and season, of the same breeding and managed as much alike as possible. Animals within a contemporary group are assigned ratios within the group by dividing individual adjusted phenotypic values by the adjusted group mean. This manipulation further reduces differences among phenotypic values in a population made up of several contemporary groups and the phenotypic value ratios can be written as:

$$P \text{ adj.} = BV + NAV + ENI.$$

The effect of these adjustments on differences among animals, along with various distributions of values, is illustrated in figure 2.

Figure 2. Distributions of values associated with performance testing concepts.

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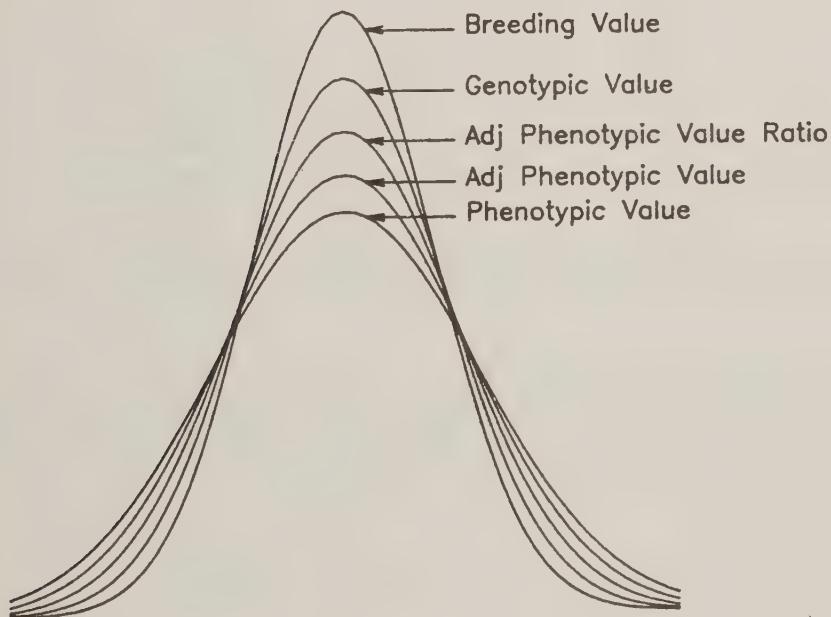
Considering the environmental variation associated with E adj. and Ecg will increase the correlation between P adj. and BV (which increases heritability) and thus increase the accuracy of the selection process.

For certain traits where multiple measures on the same animal are taken, i.e., Most Probable Producing Ability (MPPA) of cows based on weaning weights of their calves, the ENI can be partitioned into permanent and temporary environment effects.

$$ENI = Ep + Et$$

$$MPPA \text{ ratio} = \frac{G + Ep}{G + Ep + Et}$$

Evolution of the Performance Movement

There has been and still is an evolution in the "performance movement". This evolution can be divided into three phases. Initially, it consisted of recording and using individual performance measures such as weaning and yearling weights and ratios. These adjusted phenotypic values were used as a basis for selection. Secondly, this systematic recording of measures over time provided data banks; and this information, combined with pedigree information, was used to calculate estimated breeding values (EBV's). For young animals, individual performance information plus that on collateral relatives (maternal and paternal half-sibs) is used. For older animals, progeny information is added to the above as it becomes available to increase the accuracy of the estimates. In sire evaluation programs, progeny information is used to calculate expected progeny difference (EPD's), which are one-half of the breeding value. EBV's and EPD's are now calculated for birth weight, weaning weight, yearling weight, measures of calving ease and maternal breeding value. Statistical methodology has also evolved where information on all relatives of an animal can be used to estimate breeding values. The use of these EBV's and EPD's as selection criteria increases the accuracy over initial methods of using only individual or progeny information.

Presently and in the future (third phase), the genetic information provided by EBV's and EPD's will be combined with information on mating systems and environmental parameters obtained from data banks and research to develop total production systems on a herd-life cycle basis. This packaging of information will aid producers in their decision-making processes associated with beef production.

Future Considerations

The role of performance testing will still be to characterize germ plasm and identify superior seedstock. However, the emphasis will shift to identifying optimum breeding values for specific purposes rather than emphasizing maximums. Performance testing will take on a much broader scope and be integrated into the systems analysis concept.

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Additional performance traits associated with lifetime production and these areas of emphasis include:

REPRODUCTION

        Fertility--scrotal circumference, age at puberty, postpartum interval, date of calving.

        Calving Ease--birth weight, gestation length, pelvic area, and breeding values for calving ease.

GROWTH   —   Breeding values and EPD's for birth, weaning, yearling and mature weights and growth curve parameters.

MILK   —   Maternal breeding values or breeding values for milk.

CARCASS   —   Less emphasis in performance programs.

ENERGETICS —   Metabolic efficiency, cow maintenance, female body composition, appetite.

OTHER   —   Behavior, temperament, flexability.

Finally, many new, nontraditional production systems will be identified and used. Future beef cattle improvement will focus more on utilization of between-breed variation and heterosis. Emphasis will be on systems of maintaining higher levels of heterozygosity within uniform cow herd groups instead of systematic crossing schemes only. The seedstock industry will change with a larger portion coming from newly developed composites. No few composites will dominate but phenotypic look-alike, genetically different composites will be crossed to develop self-contained, combination seedstock-commercial operations.

The next decade will be interesting and challenging and changes will be rapid in the beef cattle improvement arena.

References

Baker, Frank H. 1984. A study of the beef cattle performance databanks of the United States. Winrock International.

MEASURING EFFICIENCY OF BEEF PRODUCTION

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Introduction

In this discussion, efficiency will refer to input or cost per unit of output value. Efficiency can be examined separately for cow-calf, backgrounding and feedlot operations or combined in terms of full life-cycle inputs/outputs. Efficiency also can differ between purebreeding, crossbreeding, and among integrated industry production systems involving both purebred and crossbred matings in constituent cattle populations. Biological efficiency is measured as feed energy input per unit of beef output in terms of Mcals/kg of live weight or retail product beef output from the system. Economic efficiency includes both feed and nonfeed costs in $ equivalents per unit of beef output, considering relative costs per unit of cow vs feedlot feed, values for cull cow vs feedlot market animals, and differing retail product yield and quality of live weight marketed.

Lower costs per unit of desirable beef output, of course, will result in proportionally much larger profits (or reduced losses) for beef producers, but only to the extent that market prices are not correspondingly reduced. However, lower production costs always will improve the ability of beef to compete with pork, chicken, turkey and fish for consumer demand.

Components of Efficiency

Biological Efficiency of Beef Production. Opportunities for increased efficiency can be evaluated by examining effects of performance differences on inputs required for each major phase of the life cycle. The feed energy input for life-cycle beef production can be partitioned roughly--16% for growing replacement females, 34% for cow maintenance, 8% for gestation and lactation, 23% for maintenance of growing calves from 80% of the cows, 13% for deposition of body fat and only 5 or 6% for deposition of body protein in market animals. Nearly two-thirds of the body fat and protein is in the carcass, but much of the carcass fat is removed from the retail cuts. Energy deposited in the carcass represents only 4 or 5%, and retail cuts less than 3%, of the total life-cycle feed-energy input (Dickerson, 1978; 1983).

The opportunity for beef production is based on the ability of cattle to convert the vast amounts of forages and crop residues not usable by pigs or poultry into highly nutritious and tasty human food. Contrary to occasional misleading information in the news media, about 90% of the total feed energy used in life-cycle beef production comes from pasture, harvested forages and

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by-products feed—and only 10% from feed grains added to feedlot finishing diets (Ward et al., 1977). Incidentally, this ability of feedlot beef and of other meat animals to convert surplus grain (i.e., supply above demand for export and for direct human consumption) into expanded total meat production is essential to stabilize prices for U.S. grain producers.

Species Differences Affecting Efficiency. Components of performance affecting input/output efficiency of meat production are illustrated dramatically by the performance differences among species of meat animals (table 1 and figure 1). Beef and lamb require much more feed energy per unit of meat protein output than pork or poultry, largely because of their much lower rate of reproduction but, partly, because of their greater fat deposition, slower relative growth or lower dressing percentage.

TABLE 1. MEAN PERFORMANCE TRAITS FOR SPECIES OF MEAT ANIMALS[a]

Species	Progeny/ year	Breeding weight, kg	Market weight kg	Dressing %	Daily g	Gain $g/kg^{.75}$	Carcass fat %	Biological efficiency Mcal feed Kg meat protein
Broiler chicken	100	3.0	2.0	63	31	30.5	13.0	80
Turkey	60	10	10	79	65	19.2	13.0	87
Rabbit	40	4.5	3.2	60	32	22.3	6.8	105
Pork	12	170	100	73	540	28.4	32.0	151
Lamb	1.4	70	50	50	220	18.2	36.0	427
Beef	.8	500	475	61	950	14.8	32.0	442

[a] From Dickerson, 1983.

Feed energy per unit of meat protein output for beef and lamb is about five times that for poultry meat and nearly three times that for pork (figure 1). When the lower costs of feed energy and lower ratio of feed to nonfeed costs for ruminants are taken into account (figure 2), relative total costs/unit of lamb or beef protein are lower but still roughly three times those for poultry meat and 1.4 times those for pork. The higher costs for beef and lamb relative to pork and poultry meat are largely for higher female replacement and yearly maintenance costs caused by the low reproductive rate but also for greater fat deposition relative to poultry and for slower relative growth rate compared with pigs and broiler chickens.

Clearly, efficiency of lean beef production would be increased by a higher net reproductive rate and by faster growth and reduced fat deposition in market animals.
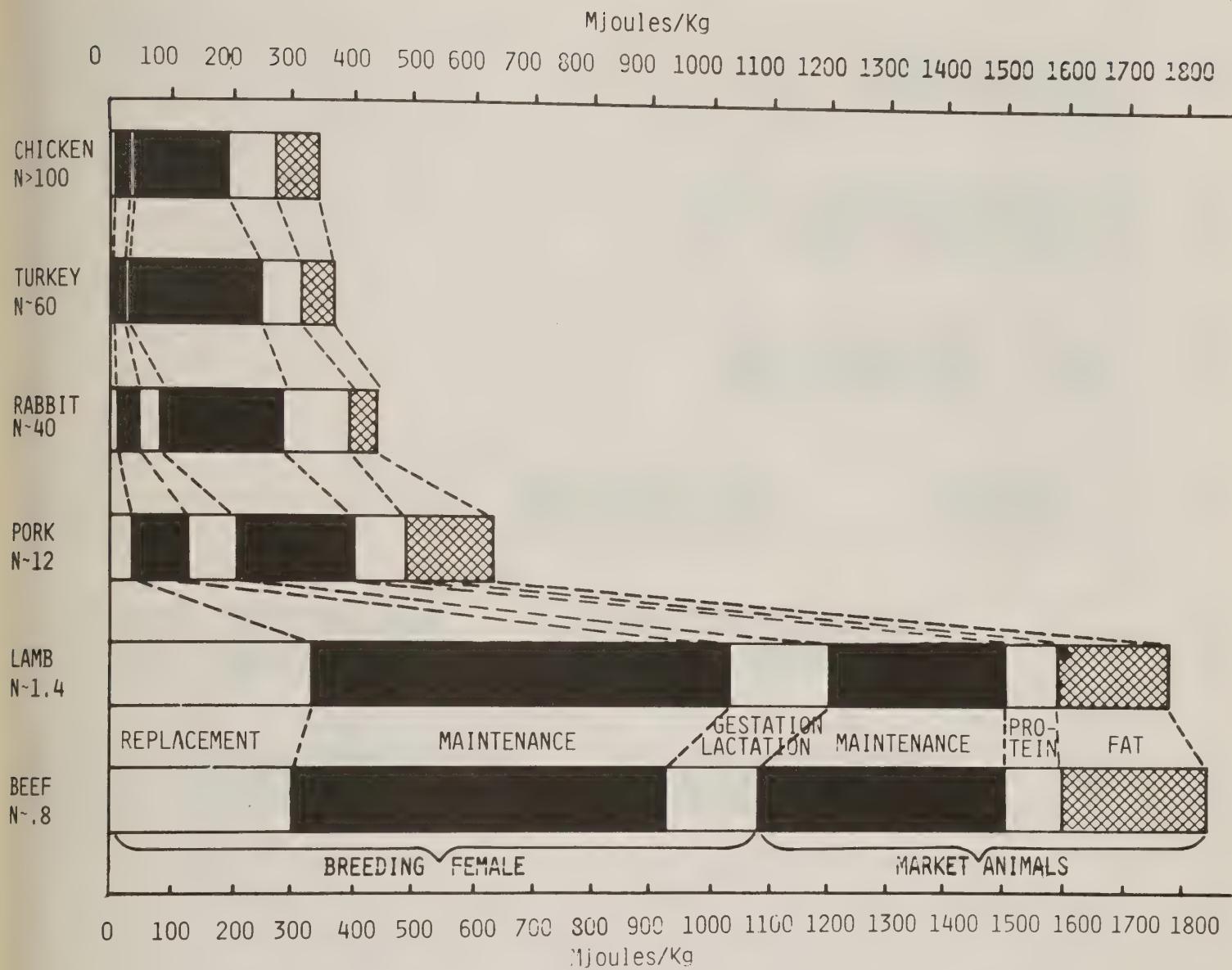
Fig. 1. Total life cycle energy intake per unit of edible meat protein output, by components of feed energy use for populations of meat animal species. (From Dickerson, 1978).
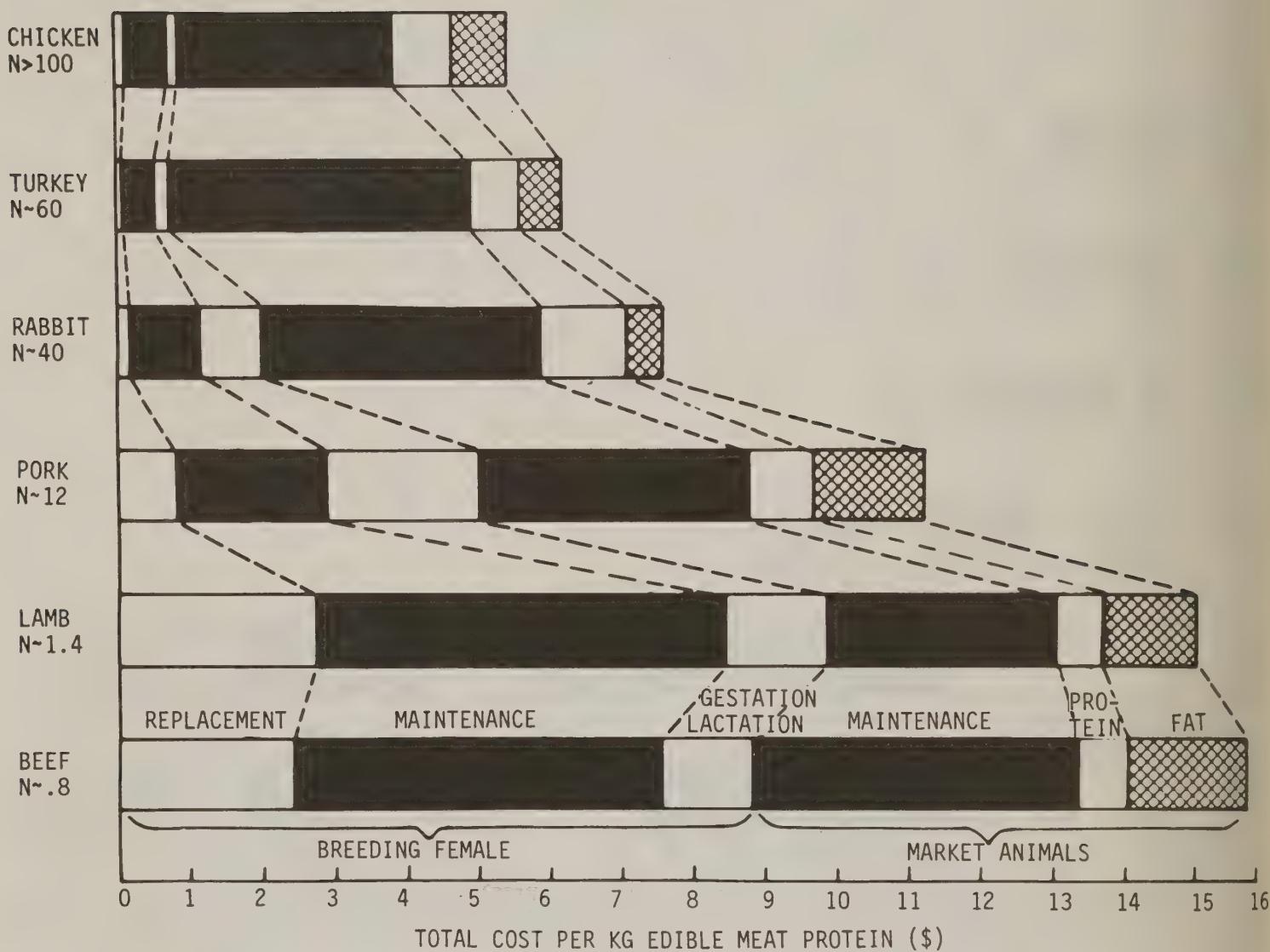
Fig. 2. Total life-cycle costs per unit of edible meat protein output, and partition by components of energy use, for populations of meat animal species ($). From data for Figure 1, assuming that non-feed costs are 150% of female energy costs plus 80% of market animal maintenance energy for non-ruminants but only 70 and 50%, respectively, for ruminants. Prices used per MJ of feed ME for breeding females and for growing market animals. respectively, were 0.956 and 1.076¢ for non-ruminants, and 0.478 and 0.717¢ for ruminants. (From Dickerson, 1978).

Performance Effects on Outputs

Past emphasis in beef improvement has focused largely on performance changes which would increase output per individual or per cow and, especially, on growth rate because it is easy to measure early in life and rather highly heritable. Output per cow maintained clearly also would be increased by earlier first calving and rebreeding, fewer open and cull cows, higher calf survival, faster growth to heavier market weights and higher dressing percentage and yields of retail cuts, as well as by larger and less fat cows marketed and, possibly, by more twins and higher milk production. The net effect on efficiency from such alternative changes in performance also depends upon how much each increases the required inputs and on the degree to which an increase in any one trait has adverse effects on other traits.

The feasibility of and most effective breeding methods for making the desired changes in performance is a challenging subject in itself and has been addressed by other speakers in this symposium and in many other publications (e.g., Dickerson and others in Yamada, 1983). Our primary purpose in this presentation is to consider methods of measuring or predicting effects of changes in performance on inputs as well as outputs and, thus, on the net efficiency of beef production.

Performance Effects on Inputs

We know that increased performance levels affect the feed and other inputs required for maintenance, gestation and lactation of cows and for maintenance and growth of both replacement females and market animals. The challenge is to predict accurately how much both outputs and inputs will increase with given changes in performance.

For Maintenance. The maintenance requirement is defined as the rate of feed energy intake required to maintain constant body weight and composition under specified conditions and is measured most directly in nonpregnant, nonlactating mature cows. Thus, the additional feed required during pregnancy and lactation can be charged to energy demands for those functions. Cold (or extreme heat) stress and increased walking required to harvest feed also can increase total feed energy required to maintain stable body energy content (NRC, 1981).

When feed intake is held below maintenance levels for extended periods, the size of the digestive tract and liver decreases (Koong et al., 1982b, 1983; Ferrell et al., 1983). Because these visceral organs are metabolically more active than muscle and even more so than fat tissue, the animal's maintenance requirement is also reduced until recovery of "normal" organ size sometime after ad libitum feed intake is resumed.

Maintenance is difficult to measure in growing animals because they tend to burn body fat but continue growth of bone and muscle when they are fed at levels to maintain body weight for extended periods. A simple estimate of the basal metabolism portion of maintenance can be obtained by measuring total body heat production of young animals after the digestive tract has been temporarily emptied by fasting only a few days.

Maintenance of normal body weight and life functions requires about 75% of
the annual feed energy of the cow herd and over 50% of that for calves from
weaning to market age (Dickerson, 1978; Ferrell and Jenkins, 1984d). Total
heat production is associated with body weight but is influenced very little
by weight of body fat (table 2). It is more closely associated with nonfat
tissue (Pullar and Webster, 1977; Webster, 1978 [table 2 from Buckley et
al., unpublished]), especially with the metabolically active visceral organs
and blood (Tess et al., 1984a; table 3 from Buckley et al.). Maintenance
feed per unit of body weight has been shown to be higher for breeds that are
inherently equipped to produce larger amounts of milk, even in growing
heifers and open, nonlactating cows (table 4, Smith and Baldwin, 1974;
Jenkins and Ferrell, 1984; Ferrell and Jenkins, 1984a,b; Buckley et al.,
unpublished).

TABLE 2. CORRELATION OF FASTING HEAT PRODUCTION WITH BODY WEIGHT AND ITS
CHEMICAL COMPONENTS BY AGES[a]

Age (mo)	Live wt (W)	$W^{.75}$	Empty body	Fat	Non-fat	H_2O	Nonfat dry	Protein	Ash
0	.74	.74	.74	.59	.73	.73	.78	.77	.73
4	.82	.82	.83	.46	.84	.84	.80	.77	.83
7	.72	.71	.66	.26[b]	.71	.70	.71	.68	.77
10	.84	.83	.81	-.13[b]	.85	.85	.80	.81	.73
14	.79	.79	.82	.20[b]	.85	.86	.80	.78	.73

[a] From Buckley et al. (unpublished) calorimetry and composition data on
6 heifers for each of five ages, 0 to 14 mo, for each of Hereford,
Charolais and Simmental breeds.

[b] $P > .10$.

TABLE 3. PARTIAL REGRESSIONS OF FASTING HEAT PRODUCTION ON EMPTY BODY
COMPONENT WEIGHTS BY AGES[a]

Age (mo)	b_0	Blood + viscera	GI tract	Head, hide, shank	Carcass
0	32.6	9.2	9.2	-8.6	4.5
4	-79.9*	25.4**	10.6**	-1.4	-.3
7	94.0	-13.6*	1.3	3.1	1.9**
10	36.4	4.7	3.0	-2.0	1.6*
14	21.3	6.2	-.5	-1.1	1.8*
Pooled/age	51.0	4.0	1.1	-1.4	1.8**

[a] From Buckley (unpublished) calorimetry and composition data on 6 heifers
for each of five ages, 0 to 14 mo, for each of Hereford, Charolais and
Simmental breeds.

* $P < .05$; ** $P < .01$.

There is evidence that some breeds (e.g., Brahman, Charolais) have lower appetites and less body fat relative to their inherent lean growth potential, but also relatively less of their body protein in visceral organs than in muscle tissue. Thus, their maintenance requirements per unit of body weight (table 4) may be similar to those of fatter breeds with higher ratios of visceral organs to muscle mass (Butler et al., 1956; Frisch and Vercoe, 1977; Ferrell and Jenkins, 1984a; Buckley et al., unpublished).

TABLE 4. ESTIMATES OF METABOLIZABLE ENERGY REQUIRED FOR MAINTENANCE OF VARIOUS BREEDS AND BREED CROSSES[a,b]

Breed of breed cross	Physiological state		Maintenance $(kcal/kg^{.75}/day)$
Angus x Hereford[a]	9-10 yr, nonpregnant, nonlactating[b]		130
Charolais-x	" " "		129
Jersey-x	" " "		145
Simmental-x	" " "		160
Angus x Hereford[a]	8-9 yr, lactating[c]		151
Red Poll-x	" " "		157
Brown Swiss-x	" " "		156
Gelbvieh-x	" " "		158
Maine-Anjou-x	" " "		146
Chianina-x	" " "		174
Angus	5-6 yr, lactating[d]		141
Hereford	" " "		149
Simmental	" " "		166
Charolais	" " "		165
Angus 5-6 yr, nonlactating[e]		86	149
Hereford	" "	99	142
Simmental	" "	166	151
Hereford	9-15 mo[f]		106
Simmental	"		126

[a] F_1's produced from Angus, Hereford, Charolais, Jersey, Simmental, Red Poll, Brown Swiss, Gelbvieh, Maine Anjou and Chianina matings on Angus or Hereford cows.

[b] Ferrell and Jenkins (1984a).

[c] Cundiff et al. (1983).

[d] Ferrell and Jenkins (unpublished).

[e] Ferrell and Jenkins (1984b) for restricted and ad libitum feed intake.

[f] Ferrell and Jenkins (1984c) for bulls and heifers.

Jacobs (1984) has emphasized literature evidence that generally total cow feed intake may be more nearly proportional to the .5 than to the .75 power of cow weight, compared to the .42 power of cow weight for predicting calf weaning weight. Thus, use of the .75 power may overestimate maintenance costs of larger cows.

For Gestation and Lactation. Extra cow feed energy costs during gestation and lactation obviously are associated with gestation length, calf size, twinning and level of milk production (table 5). Twin calves apparently do not cause cow intake of a low-energy feed to increase during the last trimester of pregnancy when gut capacity becomes limiting but do cause substantial reduction in empty body weight of cows (>45 kg) to supply the 60+% increase in energy required for fetal growth and some increase in maintenance as well (Koong et al., 1982a). Birth of twins did not delay subsequent conception (Wheeler et al., 1982) but increased milk output 30 to 50% during the first 3 mo of lactation and by 80 to 90% during the second 3 mo (Smith et al., 1982). Further data and analysis are needed to document the increased feed intake required for gestating and nursing twin calves.

Some indication of increased lactation feed requirements associated with higher milk production is shown (table 6) in the breed-cross comparisons reported by Cundiff et al. (1983). These comparisons include effects of breed differences in body size, composition and visceral vs carcass muscle distribution of body protein in addition to the large reported differences in milk production for cows fed to maintain constant body weight from 45 d to 183 d of lactation. Cow feed intake was closely associated with milk production when both were expressed per 100 kg of cow weight. However, both gain and 183-d weight of calf per Mcal of cow plus calf creep feed intake during lactation were only slightly greater for the Angus-Hereford crosses than for the higher milking Brown Swiss and Gelbvieh or the larger Maine-Anjou and Chianina crosses. These comparisons are incomplete because they do not include inputs for cows during the other 5/8 of the year, growing replacements and postweaning calf gains and on outputs of market calves and cull cows (fertility). Also, mating all cow types to the same breed of sire gives an advantage to the smaller cow types (e.g., Red Poll cross) in calf growth potential relative to cow maintenance (i.e., complementarity). Several other experiments comparing weaned calf output relative to full-year feed input (Davis et al., 1983; Dinkel, 1984b; Marshall et al., 1984; and others cited in review by Gregory, 1982) for breeds or crosses differing appreciably in level of milk production suggest that increased cow inputs from higher milk production can be offset by a proportional increase in output of calf weaned under favorable nutrient availability but that weaning efficiency declines for milk production above levels optimum for calf growth or for maintenance of cow breeding condition. The greater efficiency in utilization of milk than of creep feed energy by calves and the spreading of cow maintenance costs over more cow output both help to maintain weaning efficiency with increasing milk production.

For Growth. Daily feed energy above maintenance required for growth (ME_g) of cattle is largely determined by rate of growth, composition of gain and proportion of ruminant (dry feed) vs monogastric (milk) source of feed

TABLE 5. SINGLE VS TWIN EFFECTS ON COW FEED REQUIREMENTS

	Heifers		Cows	
	Single	Twin	Single	Twin
Gestation[a]:				
Feed ME				
($Kcal/kg \cdot ^{75}/d$)	180[b]	176[b]	167[c]	165[c]
Body wt change				
(g/d)	128[b]	−321[c]	56[b]	−409[c]
Fetal ME				
(Kcal/d)	3890[b]	6090[c]	3800[b]	6490[c]
Maintenance ME				
($Kcal/kg \cdot ^{75}$)	130	137	124	142
Lactation:				
Days to conception				
(Wheeler et al., 1982)	57[b]	69[b]	87[c]	76[c]
Milk/d (kg):				
13 wk (Pollak et al., 1978)	−−	8.5	−−	11.5
1st 3 mo	9.6[b]	12.3[d]	6.8[c]	10.1[d]
2nd 3 mo (Smith et al., 1982)	7.6[b]	14.3[d]	7.6[b]	13.7[d]

[a] Last trimester (Koong et al., 1982a).
[b,c,d] Means with different superscripts differ (P<.05).

TABLE 6. FEED REQUIREMENTS AND CALF OUTPUT FOR SIX TYPES OF CROSSBRED COWS FROM 45 TO 183 D OF LACTATION[a]

			Per 100 kg cow wt					100 calf wt/feed (kg/Mcal)[b]	
	Mean cow wt	Milk	Feed ME (Mcal)		Calf wt (kg)				
Cow breed	(kg)	(kg/d)	Cow	Creep	Mid	Gain	Final	Gain	Final
Angus x									
Hereford (A/H)	513	1.24	671	154	155	151	231	3.57	5.45
Red Poll x A/H	472	1.73	769	161	167	157	245	3.58	5.59
Brown Swiss x A/H	504	1.89	787	146	171	161	251	3.42	5.35
Gelbvieh x A/H	523	1.65	758	136	170	157	249	3.36	5.31
Maine Anjou x A/H	560	1.46	709	130	173	161	254	3.42	5.39
Chianina x A/H	557	1.14	704	132	168	154	244	3.30	5.25

[a] Calculated from Cundiff et al. (1983).
[b] Mcal of total cow feed plus calf creep feed.

intake. Because protein contains less energy than fat (5.7 vs 9.6 Kcal/g) and is deposited with lower net efficiency (e.g., ≈40 vs 78%), the post-

rumen ME requirement is similar for protein and fat (14 vs 12 Kcal/g). However, for ME intake through the rumen, net efficiency is lower for protein deposition (≈25%), thus doubling the required ME intake for protein deposition. The ME intake requirement for nonfat tissue (lean) deposition is much lower (1/5 to 1/4) than for protein because of the water content in lean and, thus, differs with age and condition as well as among tissues (Webster, 1980).

The total feed requirement for growth, of course, includes that for maintenance, which increases with the age-change in body mass. Thus, total feed/gain from birth or weaning to market for individual animals of a given mature size increases for heavier weight endpoints. But, life cycle inputs also include feed for the cow herd, which become smaller per unit of beef marketed as final market weight is increased. Thus, economically optimum market weights are partly a combination of increasing individual and decreasing cow herd feed inputs per unit of beef marketed.

For Nonfeed Costs. Nonfeed inputs are partly fixed charges per cow or feedlot animal for such items as vaccination and taxes. However, more of these costs are nearly fixed for a ranch, forage or feedlot enterprise and vary roughly in proportion to feed consumed per cow or steer (Jacobs, 1984). This tends to make biological (feed) efficiency a good predictor of economic efficiency, except as prices per unit of feed energy differ widely between cow-calf, backgrounding and feedlot phases. Thus, performance levels of management changes can cause differing effects on life-cycle economic efficiency, depending (e.g.) upon their relative impacts on cow-calf vs feedlot postweaning phases. For example, the potential advantage of terminal crossing over rotation crossing programs becomes greater as the price of feed energy for cows approaches that for feedlot calves (Notter et al., 1979c).

Predicting Efficiency from Performance

Unfortunately, actual accounting measurement of biological and economic efficiency in beef production for varying genetic levels of performance components under a representative range of beef production-marketing scenarios is not feasible. The alternative is to predict feed and nonfeed inputs and outputs and net efficiency using available information from the literature on relationships of genetic performance levels with feed and nonfeed inputs under different production-marketing systems. This is not a simple task but can be attempted at various levels of detail. Dr. T. C. Cartwright has been a pioneer in detailed simulation of beef production systems (Cartwright, 1984) and will discuss this area. I will consider only the usefulness and limitations of some approximate predictors of performance-level effects on efficiency of beef production.

Input Cost/Pound of Beef Output. A general formula, modified from Dickerson (1976), will serve to illustrate expected effects of changes in components of performance on costs/unit output.

$$\frac{\text{Input}}{\text{Output}} = \frac{\overset{\text{For breeding females (d)}}{C_{od} + F_{md} \cdot B_d + F_\ell \cdot W_w/\overline{W}_w} + \overset{\text{For progeny (p)}}{N \cdot D(C_{op} + F_{mp} \cdot B_p + F_{gp} \cdot G_p) + N_s S_p}}{N_c \cdot W_d \cdot V_d \qquad + \qquad N_s \cdot W_p V_p}$$

Where annual costs or returns per cow maintained (exposed to breeding) are:

C_{od} = for nonfeed cow items.

F_{md} = average cow maintenance feed.

B_d = metabolic cow size, relative to population mean.

F_ℓ = average cow feed above maintenance for pregnancy and lactation.

$W_w/\overline{W}_w$ = total calf weight weaned relative to population mean.

N = number of calves reared.

D = number of days from weaning to market weight.

C_{op} = average nonfeed costs per day fed postweaning.

F_{mp} = postweaning average calf feed/day for maintenance.

B_p = average postweaning metabolic size, relative to population mean.

G_p = calf postweaning gain per day, kg.

F_{gp} = average above-maintenance feed/kg of calf postweaning gain.

N_s = number of calves marketed = $N-N_r$, where N_r = number replacements = $(1-N)R + N_o + N_m$, R=rate of culling open cows, N_o = number other cows culled and N_m = number cows died.

S_p = marketing and slaughter costs/head.

N_c = number of cows culled = $(1-N)R + N_o$.

W_d = mean weight per cow culled, kg.

V_d = value/kg for cows culled relative to V_p.

W_p = mean weight per calf marketed, kg.

V_p = value/kg for calves marketed.

Differences in cost of cow vs feedlot feed would be reflected in average values of F_{md} and F_ℓ vs F_{mp} and F_{gp}.

Increasing net calf crop reared (N) raises the number of calves sold of calves reared, (N_s/N) because N_s is increased by the reduced numbers of replacements $(N_r = (1-N) R + N_o + N_m)$ through less culling for infertility or other causes and by less cow mortality. The primary effect of increasing N, however, is to reduce total breeding herd costs per unit of calves marketed in proportion to $1/N_s$.

The increase in calves marketed (N_s) is only partly offset by reduction in cows culled (N_c), so that total beef output is $(N-N_m)W_p \cdot V_p - [R(1-N) + N_o](W_p \cdot V_p - W_d \cdot V_d)$ or (market calf value x calf crop reduced by calf mortality), less the (difference in value of a market heifer vs a cull cow x proportion of cows culled). Reduced culling of cows is important (Gibb, 1984), but less so than increased calf crop and cow survival (Niswender and Wiltbank, 1984). It is difficult to visualize real circumstances that would make efficiency decline for pregnancy rates above about .8 in cow-calf feedlot operations, as simulated by Bourdon (1984). If N is increased partly by twin births, there would be some increase in amount and quality of feed for pregnancy and lactation roughly proportional to the increase in total calf weaning weight per cow exposed, $F_\ell W_w/\overline{W}_w$, as well as more days from weaning to market (D), slightly smaller postweaning mean metabolic size (B_p) and possibly slower rate of gain (G_p). If only one twin is left on the cow and the other reared artificially, postnatal cow costs would be unchanged but extra costs for milk replacer, labor and housing would be incurred along with possibly heavier combined weaning weights. If calves are sold at weaning or after backgrounding, postweaning costs would be eliminated or reduced, market weights (W_p) lowered and values (V_p) changed, compared with marketing at slaughter and the effects of increasing N on cost/unit output would become proportionally greater and primarily from reduction in cow-herd costs.

Growth Rate. Increasing calf growth rate (G_p) would be more helpful in specialized terminal sire crossing with maternal breed-cross dams (Notter, 1979b,c) than in pure or rotation breeding systems, in order to avoid the expected cow-size increase in nonfeed and maintenance costs $(C_{od} + F_{md} \cdot B_d)$, in addition to increased costs for heavier weaning (W_w/W_w) and post-weaning $(C_{op} + F_{mp} \cdot B_p + F_{gp} \cdot G_p)$ weights at a given age), that would be only partly offset by greater cull-cow returns. Faster calf growth improves efficiency much more if final market weights (W_p) are increased in proportion to weight at a fixed age than if slaughter weights are unchanged because all cow herd costs are thereby spread over more weight of beef marketed. The simulation results of Notter et al. (1979b) indicate little advantage from increasing mature cow size in rotation crossbreeding, especially if the increase in size is accompanied by later maturity but a distinct advantage from increasing only market calf growth potential, particularly when feed is relatively expensive for cow vs feedlot and if increased dystocia can be avoided by using older cows for terminal crossing.

The analyses of experimental measurements of individual annual cow-calf output/unit of ad libitum feed input to weaning or to slaughter (Dinkel, 1984; Hauser, 1984) generally show mild negative association with cow size but strong positive association with calf weaning weight and

cow milk production, and with live or retail product weight at grade- or age-constant slaughter weight. These high positive associations with individual growth rate include effects of variation in complementarity (i.e., ratio of mature size for calf's sire/dam), and in milk production and body composition under ad libitum feeding as well as individual errors of measurement and, thus, exaggerate effects to be expected from increasing average genetic growth rate and mature size in a purebreeding or rotation-crossing system of beef production.

If nonfeed costs are largely proportional to feed use (Jacobs, 1984), they would increase with feed for maintenance of larger cows plus gestation and suckling of larger calves. Feedlot nonfeed costs also are largely proportional to feed use rather than fixed per head and, thus, are roughly proportional to average postweaning calf metabolic size and days fed, $D \cdot F_{mp} \cdot B_p$.

Body Composition. Increasing only yield of lean cuts in liveweight at slaughter (V_p and V_d) would improve efficiency of purebred or rotation-cross beef production to the extent that the increased output value ($N_s \cdot W_p \cdot V_p + N_c \cdot W_d \cdot V_d$) and reduced feed cost above maintenance of leaner gains (F_ℓ and F_{gp}) more than offset increased maintenance feed for leaner cows and calves ($F_{md} \cdot B_d + F_{mp} \cdot B_p$). Presumably nonfeed costs would not increase but, thus, would be spread over more units of retail product output. Although protein deposition is energetically less efficient than fat deposition in ruminants (about 25 vs 75%), nonfat muscle tissue contains only about 20% protein and requires less than one-half as much feed energy above maintenance per unit of gain as fat (Webster, 1978; Graham, 1980; Geay, 1984). Evidence already has been presented that maintenance feed requirements would be roughly proportional to nonfat body mass, except for differences in distribution of body protein between carcass muscle and the much more metabolically active visceral organs (Ferrell and Jenkins, 1984d).

If increased lean yield is restricted to only the market calves by sires of a specialized carcass breed, adverse effects on cow-herd maintenance would be avoided and the main advantage of higher progeny output value (V_p) would be realized for the terminal-cross calves, along with lower net cost of gains (Smith et al., 1976).

Milk Production. Increased milk production alone would increase calf output (W_p at weaning). For fixed slaughter endpoints, it also would shorten the postweaning feeding period (D) but increase daily maintenance ($F_{mp} \cdot B_p$) and probably reduce daily gain (G_p) slightly depending on management and sex (Olson et al., 1978). Cow inputs for milk production ($F_p \cdot W_w / \overline{W_w}$) would be increased and, possibly, also those for maintenance ($F_m \cdot B_d$) between weaning and calving (table 4). Simulation results by Notter et al. (1979a) included expected adverse effects of increased milk on cow condition, rebreeding and calf crop and indicated that higher and wider ranges of milk production were optimum for efficiency under abundant than under poor feed resource conditions.

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Field Prediction of Efficiency. Because accurate records of feed intake are difficult to obtain, especially on pasture, various predictors of efficiency based on outputs per cow unit maintained deserve consideration for field use. Efficiency can be predicted much more accurately for a herd than for individual cows because the required information includes annual cow inventory and mortality, calf crop, culling and replacement rates, and calf weights marketed. Cow weights could also be used to remove output bias favoring larger average cow size. A "simple" field index of herd beef production efficiency for a 1-year period could be:

$$\frac{Output = N_s \cdot W_p \cdot V_p + N_c \cdot W_c \cdot V_c}{Input \quad N_e \cdot \overline{W}_e^x + N\,\overline{W}_p^x \quad A_w/12 + N_r \cdot W_r^x \, (A_e - A_w)/12}$$

where:

N_s = Number of calves marketed (beginning with breeding season).

W_p = Mean weight (kg) of calves marketed (at weaning or slaughter).

V_p = Value/kg of calves marketed (could use Value = 1 for calves).

N_c = Number of cows culled.

W_c = Mean weight (kg) of cows culled.

V_c = Value/kg of cows culled (could use V_c/V_p for equivalent calf units).

N_e = Total cows and heifers exposed to breeding.

$\overline{W}_e^x$ = Mean weight of cows and heifers exposed to breeding; x is exponent of weight proportional to feed intake usually x = .75, but x = .5 may be closer (Jacobs, 1984).

N = Number of calves weaned.

$\overline{W}_p^x$ = 1/2 $(W_w + W_o)^x$ = Mean midweight per calf from birth (W_o) to weaning (W_w), raised to power (x) proportional to feed intake.

$A_w/12$ = Mean calf age at weaning in months as proportion of year (e.g., 7/12).

N_r = Number of replacement heifers, from weaning to first breeding.

W_r^x = 1/2$(W_w + W_e)$ = Mean midweight of replacement heifers from weaning to breeding (W_e), raised to power (x) proportional to feed intake.

$(A_e - A_w)/12$ = Mean proportion of year from weaning to breeding (e.g., 8/12).

Most of the information required for such a measure of herd efficiency should be readily available for seedstock or even for some commercial beef production operations. Cow weights at breeding and calf weights at weaning easily could be predicted from heart girth tape measurements (γ = .9, Nelsen et al., 1985) if actual weights are not feasible. The more usual calculation of herd output per cow exposed would omit increased inputs for larger cows (W_e), calves ($\overline{W}_p$) and replacements ($\overline{W}_r$), and for more calves (N) or replacements (N_r). Policy on culling open and aged cows also can influence herd efficiency through N_c and N_r.

Measures of individual cow efficiency reflect mostly differences in calf weight output relative to cow feed inputs measured or predicted from cow size and calf weight (milk production), because variation in fertility and survival of cows and calves can be measured only over many parities, and culling policy naturally leaves mostly the healthy and more regular breeders in the herd (Dinkel, 1984a; Hauser, 1984).

Breed Differences in Traits Contributing to Efficiency

Genetic diversity available for use to improve efficiency of beef production can be illustrated by breed differences. Biological traits of 15 breeds, estimated from crosses with Hereford and Angus dams, are summarized for effects of calf genotype in table 7 and for those of cow genotype in table 8. These data, from three cycles of the U.S. Meat Animal Research Center Germ Plasm Evaluation Program, are based on twice the breed of sire effects, relative to the Hereford x Angus reciprocal crosses = 100 and, thus, include (2x) any deviations in specific heterosis from that for Hereford x Angus.

Among the 15 breeds characterized, note that increasing breed mature size (cow weight, table 8) was generally associated with calf genotype (table 7) for heavier birth weight, more birth difficulty and lower calf survival but with heavier weaning and 15- or 18-mo weights, higher carcass and especially retail product yield and more efficient feedlot gain in live weight and, particularly, in retail product (lean). However, larger mature size was relatively independent of cow genotype effects on performance (table 8), except for the association with heavier birth weights. Total calf weaning weight per cow exposed (table 8) combines cow fertiity and calf survival with both transmitted and maternal (milk) effects on calf growth. The major factor contributing to the wide breed of cow variation in weaning output per cow exposed (91 to 138% of Hereford x Angus) was calf weaning weight (100 to 129%), largely from milk level (80 to 210%). Variation in calf crop weaned (93 to 106%) was much less important. These measures of cow productivity ignore effects of cow body size, milking ability and body composition on preweaning inputs as well as effects on postweaning inputs and on output of retail product.

Expressing weaned calf output per unit of metabolic cow size (weight$^{.75}$ or weight$^{.5}$, table 8) roughly adjusts for breed differences in expected cow costs related to cow size but still ignores differences in cow costs related to the large breed differences in milk production (80 to 210%) and in body composition (93 to 123%, table 7) as well as their effects on feedlot inputs

TABLE 7. EFFECTS OF CALF-GENOTYPE ON COMPONENTS OF PERFORMANCE FOR BREED SAMPLES, RELATIVE TO HEREFORD-ANGUS CROSSES=100[a]

Breed of calf	Gesta-tion, d	Normal birth %	Sur-vival %	Body weight, kg				Retail product (RP,%) at 468 d		Mcal ME/kg gain 214 to 452 d age	
				Birth	200 d	452 d[b], 550 d	% offal	Carc. wt.	Live wt.	Live wt.	RF
Jersey	99	100	90	74	88	86	107.1	97.6	93.5	108	115
Sahiwal	107	93	94	112	100	94	98.3	108.4	109.5	110	101
Red Poll	101	98	101	100	98	92	100.5	100.9	100.6	117	116
Tarentaise	102	94	95	110	106	104	100.0	110.6	110.4	105	95
Hereford x											
Angus	100	100	100	100	100	100	100.0	100.0	100.0	100	100
Pinzgauer	101	93	96	128	104	104	107.3	109.4	104.8	99	94
Brown Swiss	101	89	100	118	110	108	101.5	108.4	107.5	98	90
Limousin	104	87	88	118	102	98	96.4	118.4	120.6	94	75
South Devon	102	81	91	112	100	106	98.4	104.2	105.2	97	92
Gelbvieh	102	89	88	118	114	112	100.9	110.6	110.0	94	85
Brahman	105	85	92	130	112	110	94.7	109.4	112.7	106	94
Simmental	102	75	83	126	110	116	104.5	114.2	111.4	87	87
Charolais	102	68	78	130	114	114	99.9	116.6	116.7	91	76
Maine-Anjou	101	64	87	130	112	116	96.6	111.8	113.9	95	82
Chianina	102	82	87	126	112	112	95.3	120.2	123.2	98	78
Range, %	99/107	64/100	78/101	174/130	88/114	86/116	95/107	98/120	93/123	91/117	75/116
Mean, Hereford x Angus	284	97	97	35.7	195	412	36.8	66.3	41.9	23.1	55.2

a Estimated as twice (2x) the breed of sire effect in crosses with Hereford and Angus dams. Data from Gregory et al. (1982a;b), Cundiff et al. (1982a) and Koch et al. (1982a). Includes 2x any deviation in specific heterosis effects from H x A (e.g., for Brahman and Sahiwal).

b 452 d for steers and 550 d for heifers.

TABLE 8. EFFECTS OF COW GENOTYPE ON COMPONENTS OF PERFORMANCE FOR BREED SAMPLES, RELATIVE TO HEREFORD-ANGUS CROSSES=100

Breed of cow	Cow wt 5 yr, kg[a]	Puberty (early) wk	Pregnant at 18 mo %	Calf crop Normal birth %	Calf crop born %	Calf wt, kg Birth	Calf wt, kg 200 d	Milk/d, kg	Calf viabil. %	Calf crop weaned %	Calf 200-d wt (kg) per cow exposed	Per cow wt, kg.75	Per cow wt, kg.5
Jersey	77	127	84	116	100	83	109	193	102	101	111	135	127
Sahiwal	87	68	136	131	111	76	113	187	101	106	126	140	135
Red Poll	90	111	94	98	98	107	111	143	90	94	99	107	104
Tarentaise	97	104	120	110	100	102	121	167	100	100	121	124	123
Hereford x Angus	100	100	100	100	100	100	100	100	100	100	100	100	100
Pinzgauer	101	113	128	100	104	112	115	170	100	102	120	119	119
Brown Swiss	101	114	113	112	102	111	124	170	100	101	127	126	126
Limousin	105	85	72	105	92	102	104	80	97	93	91	88	89
South Devon	108	104	82	95	96	110	107	113	109	101	110	104	106
Gelbvieh	109	117	114	105	109	109	124	170	98	104	132	124	126
Brahman	109	60	125	131	109	93	129	210	98	104	138	129	132
Simmental	111	99	84	91	94	110	121	167	104	98	117	108	111
Charolais	123	85	72	95	96	114	112	80	97	95	104	89	90
Maine-Anjou	123	100	116	105	107	123	120	110	98	102	125	107	113
Chianina	123	85	96	112	104	120	120	100	100	102	125	107	113
Range in %	77/123	60/127	72/136	91/136	92/111	76/123	100/129	80/210	90/109	93/106	91/138	88/140	89/135
Mean, Hereford x Angus	500	51	87	87	85	38.7	210	5.5	92	84	177	105.8	22.36

a Estimated as twice (2x) the effect of cow's breed of sire on her performance in crosses with sires of the same other breeds. Data from Gregory et al. (1982b) and Cundiff et al. (1982b). Includes 2x any deviation in specific heterosis effects from H x A (e.g., for Brahman and Sahiwal).

and on output of retail product at slaughter. Extra cow and calf feed inputs for inherently higher milk production may tend to be nearly proportional to the increased output of calf weaned, as reported by Davis et al. (1983), Dinkel (1984b) and Marshall et al. (1984). Extra inputs for leaner types of cows, however, would be balanced only by considering the improved efficiency for higher yields of final retail product.

The array of breed characteristics leading to maximum beef production efficiency is likely to differ for breeds used in rotation crossing compared with breeds to be used in maternal or in terminal-sire roles of cross-breeding systems. A continuing challenge to all of us is development of beef production models capable of predicting with reasonable accuracy what combinations of biological traits will permit most efficient beef production for differing production-marketing systems and for alternative breed roles in those systems. Characterizing of biological types (breeds) is important but improved methods for interpreting and utilizing such information are needed if the beef industry is to fully benefit from the effort.

Summary

Major factors influencing the production costs for beef relative to other meats were reviewed. Potential changes in biological traits of economic importance were evaluated in terms of expected effects on feed and nonfeed inputs as well as on live weight and lean beef output, including associated effects on other traits. A general formula was presented for predicting changes in the input/output efficiency of beef production from improving components of reproductive rate, growth rate, body composition or milk production. A simpler formula was presented for predicting yearly herd efficiency of beef production in terms of beef output per unit of total feed input, based upon inventory of cows exposed, culling and replacement rates, numbers, weights and relative prices for calves and cows sold—plus numbers and mean sizes of preweaning calves and replacement heifers maintained. Breed of sire effects on calf and cow biological traits were used to illustrate breed differences that contribute to beef production efficiency in rotation crossing or in maternal or paternal breed crossing roles.

Literature Cited

Bourdon, Richard M. 1984. The meaning and expectations of total management systems. In: H. Ritchie and D. Hawkins (Eds.) Proc. Beef Cow Efficiency Forum. pp 116-124. Michigan State Univ., East Lansing.

Butler, O. D., R. L. Reddish, G. T. King and P. L. Simms. 1956. Factors contributing to the difference in dressing percentage between Hereford and Brahman x Hereford steers. J. Anim. Sci. 15:523-528.

Cartwright, T. C. 1984. Evaluating beef management systems. In: H. Ritchie and D. Hawkins (Eds.) Proc. Beef Cow Efficiency Forum. pp 133-141. Michigan State Univ., East Lansing.

Cundiff, L. V., R. M. Koch and K. E. Gregory. 1982a. Characterization of breeds representing diverse biological types:postweaning growth and feed efficiency. Beef Res. Prog. Rep. No. 1 ARM-NC 21, USDA pp 1-11.

Cundiff, L. V., K. E. Gregory and R. M. Koch. 1982b. Germ Plasm Evaluation Prog. Rep. No. 10, NC-21, USDA pp 1-11.

Cundiff, L. V., C. L. Ferrell and T. G. Jenkins. 1983. Output/input differences among F_1 cows of diverse biological types. J. Anim. Sci. 51(Suppl. 1):48. (Abstr.)

Davis, M. E., J. J. Rutledge, L. V. Cundiff and E. R. Hauser. 1983. Life cycle efficiency of beef production. I. Cow efficiency ratios for progeny weaned. J. Anim. Sci. 57:832-851.

Dickerson, G. E. 1976. The choice of selection objectives in meat producing animals. In: D. Lister, D. N. Rhodes, V. R. Fowler and M. F. Fuller (Eds.) Meat Animals Growth and Productivity. NATO Advanced Study Institute, Series A Life Sciences. pp 449-467. Plenum Press, New York.

Dickerson, G. E. 1978. Animal size and efficiency-basic concepts. Anim. Prod. 27:367-379.

Dickerson, G. E. 1983. Potential genetic improvements in the efficiency of beef production. In: Y. Yamada (Ed.) Strategies for Most Efficient Beef Production. pp 85-120. Proc. of Internat'l Symp. on Beef Production, Kyoto University, Kyoto, Japan.

Dinkel, C. A. 1984a. Energetics from birth to slaughter. In: H. Ritchie and D. Hawkins (Eds.) Proc. Beef Cow Efficiency Forum. pp 38-46. Michigan State Univ., East Lansing.

Dinkel, C. A. 1984b. Range cow size. In: Proc. Fort Keogh Beef Research Symposium.

Ferrell, C. L. and T. G. Jenkins. 1984a. Energy utilization by mature non-pregnant, non-lactating cows of different types. J. Anim. Sci. 58:234-243.

Ferrell, C. L. and T. G. Jenkins. 1984b. A note on energy requirements for maintenance of lean and fat Angus, Hereford and Simmental cows. Anim. Prod. (Accepted).

Ferrell, C. L. and T. G. Jenkins. 1984c. Energy utilization by Hereford and Simmental males and females. Anim. Prod. (Submitted).

Ferrell, C. L. and T. G. Jenkins. 1984d. Cow type and the nutritional environment: nutritional aspects. J. Anim. Sci. (Accepted).

Ferrell, C. L., J. A. Nienaber and L. J. Koong. 1983. Effects of previous nutrition on maintenance requirements and efficiency of feed utilization of growing lambs. J. Anim. Sci. 58(Suppl. 1):431.

Frisch, J. E. and J. E. Vercoe. 1977. Food intake, eating rate, weight gains, metabolic rate and efficiency of feed utilization in Bos taurus and Bos indicus crossbred cattle. Anim. Prod. 25:343.

Geay, Y. 1984. Energy and protein utilization in growing cattle. J. Anim. Sci. 58:766.

Gibb, J. P. 1984. Functional traits affecting cow efficiency. In: H. Ritchie and D. Hawkins (Eds.) Proc. Beef Cow Efficiency Forum. pp 54-62. Michigan State Univ., East Lansing.

Graham, N. McC. 1980. Variation in energy and nitrogen utilization by sheep between weaning and maturity. Australian J. Agr. Res. 31:335.

Gregory, K. E. 1982. Breeding and production of beef to optimize production efficiency, retail product percentage and palatability characteristics. J. Anim. Sci. 55:716-726.

Gregory, K. E., L. V. Cundiff and R. M. Koch. 1982a. Characterization of breeds representing diverse biological types:preweaning traits. Beef Research Program Progress Rep. No. 1, ARM-NC-21, USDA pp 7-8.

Gregory, K. E., L. V. Cundiff and R. M. Koch. 1982b. Characterization of breeds representing diverse biological types:postweaning growth and puberty of females. Beef Research Program Progress Rep. No. 1, ARM-NC-21, USDA pp 9-10.

Hauser, E. R. 1984. Efficiency during the life cycle of beef cows. In: H. Ritchie and D. Hawkins (Eds.) Proc. Beef Cow Efficiency Forum. pp 77-83. Michigan State Univ., East Lansing.

Jacobs, V. E. 1984. Economic efficiency in beef production. In: H. Ritchie and D. Hawkins (Eds.) Proc. Beef Cow Efficiency Forum. pp 101-115. Michigan State Univ., East Lansing.

Jenkins, T. G. and C. L. Ferrell. 1984. Output/input differences among biological types. In: H. Ritchie and D. Hawkins (Eds.) Proc. of Beef Cow Efficiency Forum. pp 15-37. Michigan State Univ., East Lansing.

Koch, R. M., L. V. Cundiff, K. E. Gregory and M. E. Dikeman. 1982a. Characterizations of breeds representing diverse biological types: carcass and meat traits of steers. Beef Research Progress Rep. No. 1, ARM-NC-21, USDA pp 13-15.

Koch, R. M., L. V. Cundiff and K. E. Gregory. 1982b. Critical analysis of selection methods and experiments in beef cattle and consequences upon selection programs applied. In: C. L. de Cuenca (Ed.) Proc. 2nd World Congress on Genetics Applied Livestock Prod. Vol 5:514-526. Madrid, Spain.

Koong, L. J., G. B. Anderson and W. N. Garrett. 1982a. Maternal energy status of beef cattle during single and twin pregnancy. J. Anim. Sci. 54:480.

Koong, L. J., C. L. Ferrell and J. A. Nienaber. 1982b. Effect of plane of nutrition in organ size and fasting heat production in swine and sheep. In: Energy Metabolism in Farm Animals. EAAP Publ. No. 29:245.

Koong, L. J., J. A. Nienaber and H. J. Mersman. 1983. Effects of plane of nutrition in organ size and fasting heat production in genetically obese and lean pigs. J. Nutr. 113:1626.

Marshall, D. M., R. R. Frahm and G. W. Horn. 1984. Nutrient intake and efficiency of calf production by two-breed cross cows. J. Anim. Sci. 59:317-328.

Nelsen, T. C., R. E. Short, W. L. Reynolds and J. J. Urick. 1985. Palpated and visually assigned condition scores compared with weight, height and heart girth in Hereford and crossbred cows. J. Anim. Sci. 60:363-368.

Niswender, G. D. and J. N. Wiltbank. 1984. Realistic limits on reproduction in beef cows. In: H. Ritchie and D. Hawkins (Eds.) Proc. Beef Cow Efficiency Forum. pp 47-53. Michigan State Univ., East Lansing.

Notter, D. R., J. O. Sanders, G. E. Dickerson, G. M. Smith and T. C. Cartwright. 1979. Simulated efficiency of beef production for a midwestern cow-calf-feedlot management system.
a.   I. Milk production. J. Anim. Sci. 49:70-82.
b. II. Mature Body size. J. Anim. Sci. 49:83-91.
c. III. Crossbreeding systems. J. Anim. Sci. 49:92-102.

NRC. 1981. Effect of Environment on Nutrient Requirements of Domestic Animals. National Academy Sciences, Washington, DC.

Olson, L. W., L. V. Cundiff, G. E. Dickerson and K. E. Gregory. 1978. Maternal heterosis effects on postweaning growth efficiency. J. Anim. Sci. 46:1529-1538.

Pullar, J. D. and A. J. F. Webster. 1977. The energy cost of fat and protein deposition in the rat. British J. Nutr. 37:355-363.

Smith, N. E. and R. L. Baldwin. 1974. Effect of breed, pregnancy and lactation on weights of organs and tissues of dairy cattle. J. Dairy Sci. 57:1055.

Smith, G. M., D. B. Laster, L. V. Cundiff and K. E. Gregory. 1976. Characterization of biological types of cattle. II. Postweaning growth and feed efficiency of steers. J. Anim. Sci. 43:37-47.

Smith, S. P., E. J. Pollak and G. B. Anderson. 1982. Maternal influence on growth of twin and single calves. J. Anim. Sci. 55:533.

Tess, M. W., G. E. Dickerson, J. A. Nienaber and C. L. Ferrell. 1984a. The effects of body composition on fasting heat production in pigs. J. Anim. Sci. 58:99-110.

Tess, M. W., G. E. Dickerson, J. A. Nienaber, J. T. Yen and C. L. Ferrell. 1984b. Energy costs of protein and fat deposition in pigs fed ad libitum. J. Anim. Sci. 58:111-122.

Ward, G. M., P. L. Knox and B. W. Hobson. 1977. Beef production options and requirements for fossil fuel. Science 198:265-271.

Webster, A. J. F. 1978. Prediction of the energy requirements for growth in beef cattle. World Rev. Nutr. Diet. 30:189.

Webster, A. J. F. 1980. The energetic efficiency of growth. Livestock Prod. Sci. 7:243.

Wheeler, M. B., G. B. Anderson, R. H. BonDurant and G. H. Stabenfeldt. 1982. Postpartum ovarian function and fertility in beef cattle that produce twins. J. Anim. Sci. 54:589.

Yamada, Y. (Ed.) 1983. Strategies for Most Efficient Beef Production. Proc. Internat'l. Symp. on Beef Production. 510 pp. Kyoto University, Kyoto, Japan.

SYSTEMS ANALYSIS OF BEEF CATTLE PRODUCTION[1]

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Introduction

This symposium on breeding beef cattle has been organized with implied assumptions: (1) that a range environment imposes a special set of conditions for breeding beef cattle, and (2) that many factors interplay to affect productivity of beef cattle. Of the three usual phases of beef production, cow-calf, stocker and finishing, the cow-calf phase is predominant in range production although some stocker activity is also included. Nevertheless, performance levels in all phases are related environmentally and genetically and must all be considered in beef cattle breeding.

The importance of the cow-calf phase is placed into perspective by considering the basic functions of beef cattle:

  I. Reproduction - increase in numbers.

  II. Growth and maturing - increase of weight and finish.

The cow-calf phase accounts for all of the reproduction and about one-half of the weight production in the form of weanling calves and cull cows. There is little question about the importance of the cow-calf phase in the total beef production system (Cartwright, 1970).

However, there is concern about the economic viability, or lack of it, of cow-calf production and how economic returns reflect on the total production system and on beef cattle breeding. Beef consumption per capita in the U.S. has decreased but population increase has compensated so that the total demand is fairly stable. These trends indicate that there will be little opportunity for profit riding on the crest of an increasing demand; but rather, in order to realize continued profit, adjustment must be made to a mature industry where increased production efficiency is required to realize profit. In order to put the beef cattle production efficiency question in an economic context, the results of an economic analysis of a cow-calf operation in Texas (Doren et al., 1984) is used to illustrate this dimension that should not be overlooked. These results were from Texas Agricultural Experiment Station cooperative research with a large ranch where forage and cattle production data were collected over a number of years. We simulated productivity of this herd as part of our systems analysis research, first validating the observed production as a baseline and then examining the effect of a number of different optional production-management practices. Table 1 summarizes some of the results of the economic analysis.

Two points are apparent for this ranch study. One is that there was no apparent way in 1982 to make a profit with this cow-calf operation if all expenses are considered. A second is that the practices employed do have a large effect on return; that is, the practices employed do make a difference.

A third point that may be inferred is that beef cattle production is not necessarily entered into as a commercial enterprise separated from other interests. Of course, we all hope for better times; but we should be realistic and acknowledge that there are some extraneous elements holding many cow-calf enterprises together. These include use of land to provide employment or other benefits to the owner, tax shelter, tax shield, investment speculation and personal satisfactions. These factors indirectly affect production efficiency, and it is useful to recognize the base from which economic return is contemplated since the base conditions management and selection decisions. There are changes in the ranking of different management practices reported in table 1 for net return depending on the basis for figuring net returns. There are also changes in ranking based on net returns vs cattle production measures such as sale weight/cow or sale weight/feed utilized, whether the ratio is put in monetary terms or left as weights. That is, if we define the production objective in terms of net revenue, an economic analysis is then required or we may be misled by using indicators. Nonetheless, it is useful to consider production or output (O) and costs or input (I). It appears clear that emphasis needs to be placed on both decreasing costs or expenses and on increasing output or production.

TABLE 1. NET RETURNS SIMULATED FOR A COW-CALF OPERATION; 162-HA RANCH, APPROXIMATELY 100 COWS; CALVES SOLD AT WEANING; BASED ON 1982 PRICES[a]

Net revenue returns[b]	Net revenue range for different production practices[c]
Over total production costs	-$9,800 to -$7,720
To land	-$4,620 to -$2,520
To land and livestock	$2,220 to $4,940
To land, livestock, labor, management	$7,820 to $10,840

[a] Taken from Doren et al. (1984). These figures are scaled down to a 162-ha ranch for convenience of presentation and may be slight overestimates.

[b] The first line indicates returns when all production costs are included (prevailing rental fees were used for land cost); the second line is return when all costs except land are included; the third line is return when all costs except land and livestock are included, etc.

[c] The practices included different winter feed supplementation and breeding/calving season. In every case, the lower figure was for the practices actually employed on the ranch.

Beef Cattle Production

Cattle selection and breeding should be directed toward both increasing the numerator and decreasing the denominator of the O/I fraction. For convenience, I have divided traits into two categories (Cartwright, 1982):

Primary traits	Secondary traits
Size/age	Anatomical soundness
Maturing rate/size	Reproduction
Milk production	Sex organs
	Calving ability
	Muscle and bone
	Structure
	Ratio or balance
	Color
	Horned/polled
	Genetic defects
	Physiological soundness
	Adaptability to production resource
	Climate
	Nutrition
	Range area
	Disease/parasites
	Reproduction
	Hormonal balance
	Calving ability
	Temperament

Muscle/bone/fat proportions and distribution should perhaps be listed under primary traits; but for this discussion, I am avoiding that issue and looking at these only from the soundness point.

Primary traits (the traits of production) tend to predominate and mediate many other traits. They have pervasive, important correlated effects; that is, they affect—or are affected by—many other traits. Size is a composite character conveniently characterized by body weight at maturity, at a given body composition, especially fat and fill; taken relative to age, it includes rate of gain. Generally, as genetic size potential increases, rate of gain potential increases and degree of maturity, including degree of finish, at any age, decreases. Cow size is important because of effects on her growth rate, maturing rate and weight and, therefore, on feed requirements (stocking rates) for maintenance and growth and age at first calf. The nutrients consumed (including pasture/range) by cows are the major expense related to beef production (Johnson, 1984). Cow size is genetically important because of its transmitted effect on growth and maturing rates on her progeny. Level of milk production affects nutrient requirements, degree of fatness and breed-back of the cow as well as weaning weight and finish of her calf. Maturing rate, independent of size, affects age at puberty and degree of finish at any age and, therefore, age at first calf and breed-back of heifers and cows.

Size and milk production potentials can be relatively easily changed by selection. Maturing rate, independent of size, is much more difficult to measure and change by selection. Breeds exist which combine various size and milk production potentials and, to some degree, different maturing rates relative to size.

The traits listed as secondary are intended to reflect mostly structural and physiological soundness and are secondary because of generally more limited or confined effects on the primary, or production, traits and tend to have fewer correlated effects. These traits are not necessarily secondary in selection importance.

Traits that contribute positively to the reproductive phase of cow production are often not the same and may be antagonistic with those traits that contribute to growing and finishing steers. If the sire breed in a terminal crossing program is thought of as contributing to desired slaughter progeny traits, and the dam breed is thought of as contributing to reproduction, the traits desired tend to contrast (Cartwright, 1970):

Sire breeds	Dam breeds
High rate of gain	High fertility
Efficient feed conversion	Desired milking qualities
High cutout percent	Early puberty
Tender, palatable beef	General soundness
	Adaptability
	Easy calving ability
	Low feed requirements
	Longevity

This contrast illustrates that the entire production system must be examined as a whole in order to account for, and best accomodate, the interactions and "trade offs" inherent in beef cattle production systems. Since the individual animal is the usual unit of measurement and selection, we tend to think of measuring production efficiency in terms of adding up contributions of individual animals. Most selection programs for beef cattle are based on individual performance—mostly size/age. The fact is that in this case, as in many, the parts do not sum to the whole. The population, to use an animal breeding term, has characteristics of its own. After trying several approaches toward rationalizing this dilemma as beef cattle breeders, we evolved to a systems analysis approach.

Systems Analysis

The term "system" has been used in many different contexts (e.g., grazing systems). In current usage, "systems analysis" is generally accepted to refer to construction and use of a mathematical model to examine properties of a system, where "system" refers to a set of interacting bodies under the influence of related forces. Implied in this definition is that the system is broadly inclusive but bounded by definite limits. Systems analysis may be defined as the process of examining an activity by mathematical means in order to define its goals or purposes and to discover operations and procedures for accomplishing them more efficiently (Spedding, 1979).

Simulation Model. We implemented our systems analysis approach to beef cattle breeding in a straightforward, if cumbersome, manner by modeling cattle to respond to their nutritional and management environment mediated

by their genetics for the primary traits. This simulation model is programmed in FORTRAN IV, rather than a simulation language, and is based on cause and effect of biological processes to the extent we could do so. The model is structured to simulate growth, maturing, reproduction and lactation of individuals in a herd, from birth to death or sale, as a response to their environment similar to the manner in which a real herd of cattle would perform on a given range with a given management regime (Sanders and Cartwright, 1979a; b).

The Texas A&M Beef Cattle Simulation Model has a top-down hierarchial organization of 50 subroutines (Doren et al., 1984). The system simulated is the individual animal (Baker, 1982), and the animal records are handled in a circular, doubly-linked list with pointers set to designate herds or class/mating groups (D. W. Mayfield, unpublished manuscript). Stochastic elements are associated with birth, death, estrus, conception and removal.

Forrester (1968) outlined methods for defining systems through the identification of feedback loops stating that "The feedback loop is the basic structural element in systems. Dynamic behavior is generated by feedback." Figure 1 represents the feedback loops found in the model.

The levels, or integrations, in the model are weight, structural size (WM) and herd size. An example of a feedback loop is illustrated by the information flow from WM to the daily gain in WM (GWM), the rate which determines the amount of increase in WM for the month. This loop indicates that GWM is dependent upon WM(t) where t is time in months.

However, GWM is also dependent upon the genetic potentials for mature size (WMA) and maturing rate (MATR), time constants (T1 = 1 d, T2 = 1 mo [30 d]), a tabular function (FUNC) and other adjustments. WM is represented by one of two functions used over distinct intervals, which are dependent upon age (Sanders and Cartwright, 1979b). Therefore, FUNC is used to determine whether GWM is designated as a constant, implying no direct dependence upon WM (i.e., the information flow from WM to GWM is 0) or, if it is a self-limiting rate which is proportional to the difference between $WM^{(t)}$ and WMA, the amount of growth potential remaining in the individual at that time. Even if GWM is a constant, a feedback exists from WM through nutritional requirements (REQ) to GWM. If the TDN required for GWM in an individual of size WM(t) is severely limited, GWM may then be reduced (representing stunting).

The time constants, T1 and T2, are necessary to maintain consistency of units in the equations and to determine the timing characteristics of the simulation. T1 is used as a constant to determine GWM and the daily gain in weight (DW), but its more subtle utility lies in designating the interval over which a given amount of TDN is converted to live weight gain. However, the timing of events in the model occur at 1-mo intervals; thus, T2 is required to set the rates and delays on that time scale and to increment age (AGE).

Two auxilliary variables are used to determine the effects of lactation in the model; LACT1 representing the lactation of an individual and LACT2

representing the lactation of the dam of an individual. LACT1 is dependent upon a parameter (PMA) used as an index of the genetic potential for milk production, among other features.

Sales and cull functions, as well as the auxiliary variable DEATH, determine removals while FERT determines additions to the herd. The sales and cull functions are the sources of much of the influence which external management practices (e.g., stochastic elements associated with age at culling, number of heifers retained, season of weaning, etc.) have in the model. FERT is also directly influenced by management practices (minimum age at exposure to breeding, months of breeding season) and not only increments the accumulation delay (ACC) but also represents the reproductive status of the individual. The value of DEATH is determined by stochastic elements, which are dependent upon the month of the year, AGE and condition (WEIGHT/WM) of the animal, among other factors.

DEATH, FERT and the sales and cull functions are unique in that their roles transcend levels of the hierarchy in the model. The output from these variables and functions are interpreted in both the individual and herd level dynamics. This interpretation is made possible through use of tabled values of individual animal attributes that are contained in IAA. The contents of IAA are altered at the end of each month by the table UPDATE. The information flow from HERD SIZE to IAA does not constitute a pathway for a feedback through any of the components on the individual level of the hierarchy. The mechanism that limits HERD SIZE is the array size set for individual records in the computer program.

The delays in figure 1 (D1), over a given time interval, T2, produce an output signal with an instantaneous rise and decay. ACC will accumulate the number of births (or incoming animals, NA) which occurred in a given month but will not "discharge" into HERD SIZE until the end of the current month of simulation. The same type of behavior is observed for the output rates (OR1, OR2 and OR3) but the influencing factors are deaths, culls and sales (DCS).

The cloud-shaped structures in figure 1 represent either sources or sinks. The material which flows from a source to WM through GWM could be nutrients from forage and other feeds. The production of the forage or how it is made available to an individual animal is not a part of the system which this model simulates; therefore, any forage or other feed input to the system is represented as arising from a source. Outputs from the system (deaths, culls and sales) are placed in sinks.

The computer model requires input values which designate forage quality (digestibility and crude protein content) and availability on a monthly basis. These values do not change in response to behavior of the system but influence behavior within the system. Management practices can be considered disturbances since they are represented as parameters which are set outside the feedback structure of the system.

The purpose of this model is to describe a system involving the growth, reproduction and lactation of beef cattle. The information which is

Figure 1. Major feedbacks in the Texas A&M Beef Cattle Simulation Model.

Sources or sinks
Levels
Rates .
Delays (first order)
Auxiliary variable
Table
Additional information or functions
Parameters
Information flow
Material flow

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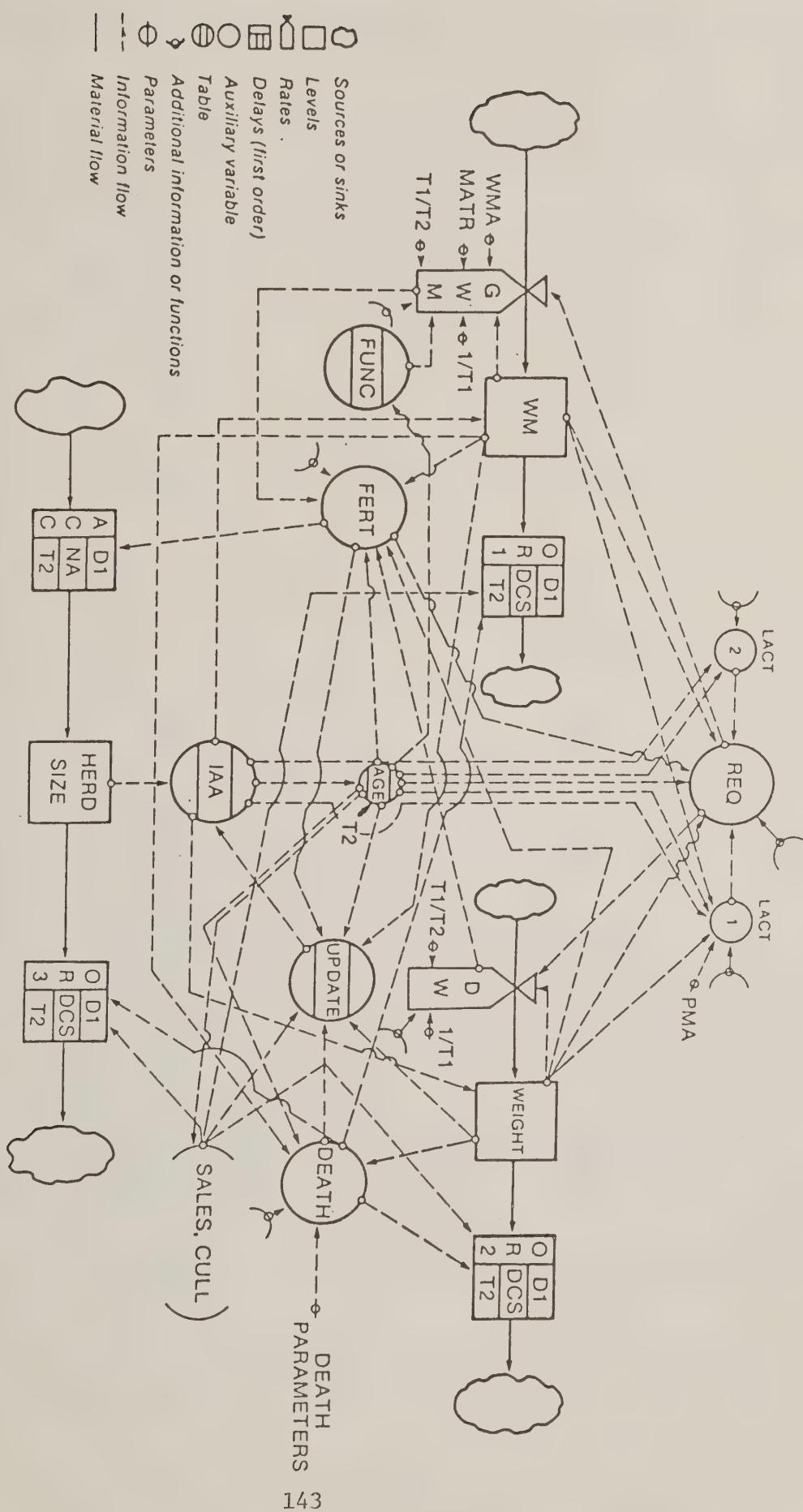
obtained from it relates to the response behavior of the system to specified inputs or disturbances (genotypes, management and feed resource).

Simulations. The first set of simulations for any given production environment is used for the purpose of validating the model for that particular production situation. A set of production data collected from a real herd of cattle in the production environment is used for the validation comparison. This set provides a method for testing the assumptions that are incorporated in the model and to determine if they hold under the conditions of the production situation. The assumptions include the set of input forage parameters (in terms of digestibility, crude protein and availability for each month), input cattle parameters (size, maturing and lactation for the breedtype) and management parameters. When there is general, close agreement between the simulated results and the actual data, the model is assumed validated and the effects of alternative inputs may then be examined with the model. However, if there is not close agreement with any production measure, reassessment of the assumptions of the model may be required and, in that case, changes in the model or inputs are made so that the model more accurately reflects the system which it is intended to represent.

Generally, our systems analysis research that has examined total offtake of a herd in relation to the production resource (characteristics of the geographic area, management, etc.) indicates that, for most cases, as the level of nutrition increases in both quality and quantity as well as the stability of nutrition through the season of the year, the size/age, maturing rate/size and milk production level that are best, or optimal, tend to increase and vice versa. That is, there is a size, maturing rate and milk production level that best fits each set of conditions and production system (e.g., cow-calf vs cow-calf-stocker-finisher, straightbreeding vs crossbreeding, intensive vs extensive). Figure 2 illustrates this point (Baker, 1982). Of the two breeds illustrated, the breed (B) with the lower "productive potential" was more efficient in total herd offtake per unit of TDN utilized under the more limited nutrition. When the nutrition was improved to a level that better supported a faster maturing, larger cow that gave more milk, the breed ranking reversed and breed (A) with the higher potential was more efficient. The management, breeding and production system must be synchronized. Few agricultural commodities are produced under a wider array of conditions than cattle, especially cow-calf production. No single set of recommendations is best for every producer.

In general terms, it seems safe to recommend for range beef cattle that emphasis should be placed on getting cattle within the optimal bracket for the primary traits for the production conditions; i.e., select cattle so they are close to the best or optimal size, maturing rate and milk production. Then, begin shifting emphasis to the secondary soundness traits thinking about production costs with easy keeping or low-care cattle. For example, calving difficulty present at even a low level in range cows can overwhelm breeding improvements we may make for production characters.

The major effects interacting with breeding are nutrition, weather and market. The weather and market (or price of cattle) are extraneous effects in that they don't respond to individual producers' efforts, the producer must

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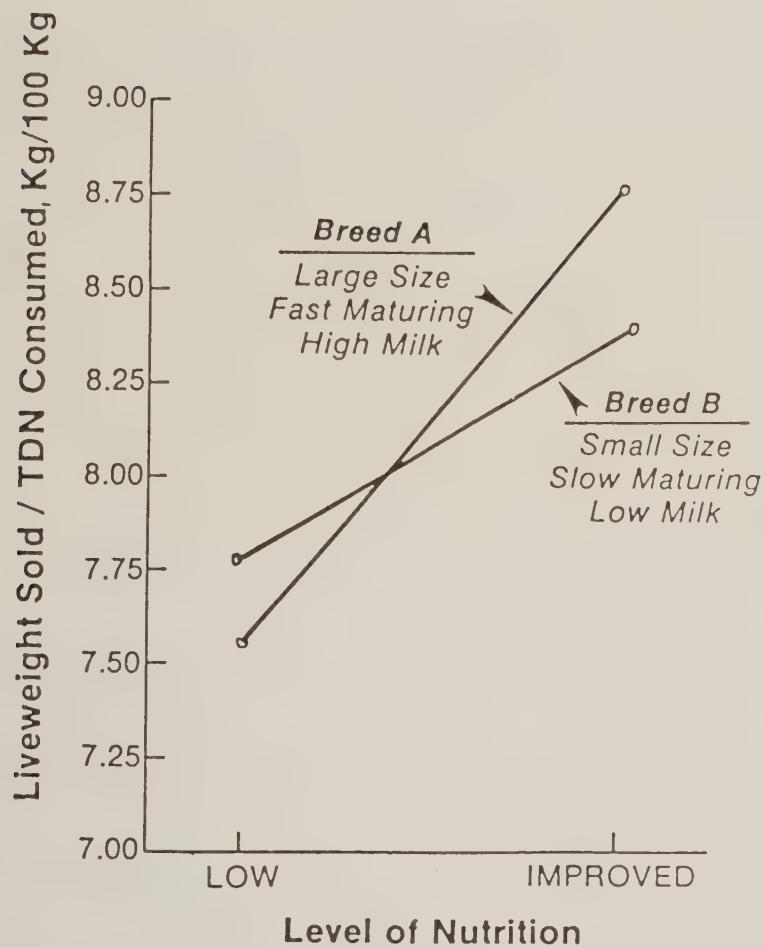
Figure 2. Simulated net herd efficiency, as measured by liveweight offtake per 100 kg of TDN consumed, of two breeds contrasting in genetic potential for three primary characters, simulated as breed A and breed B kept on a generally low quality, seasonally variable range and then again on the same range with modest feed supplement added during the period of lowest quality and lowest production of forage. The data for the simulations were taken from a ranch in the Gulf Coastal Plains area of Texas.

respond to them. A cow-calf producer can only develop a strategy to attempt to cope with these facts of life; generally, that means reducing his risks.

The greatest nutritional problem in cow-calf operations is coping with the seasonal nature of feed (pasture/range) supply. As grain and other harvested feeds (e.g., hay and silage) become more expensive relative to the price of cattle (which is a likely long-term trend), then the problem becomes greater.

Winter feeding is the problem of most concern for a large portion of Texas producers, and I think most other producers. We have examined through our systems analysis research the best level of winter hay feeding in several areas. One is northeast Texas where a lot of Coastal bermudagrass hay is grown and winter hay feeding is almost univerally practiced. Data were taken from experiments at the Texas Agricultural Experiment Station Research Center at Overton (Nelsen et al., 1982). The effects of feeding hay at levels from almost starvation to ad libitum during the winter were simulated. The effects of different winter hay feeding on cow herd production are shown in table 2. The hay quality simulated for study was of the low quality typically produced in that area; the digestibility of the hay was approximately 55% as fed. Price relationships were compiled for a long term extending from the 1950's through the 1970's. Feeding cows at the level of about 80% of ad libitum (about 8-9 kg/day for a mature cow) was the most economical practice. It is evident from the conception rates and weaning weights that the cows on this pasture resource could not recover sufficiently from a large winter weight loss in order to produce efficiently.

TABLE 2. SIMULATED AVERAGE COW HERD PRODUCTION FROM DIFFERENT LEVELS OF WINTER HAY FEEDING[a]

Cow herd performance	Level of hay feeding[b]			
	Unlimited	80%	60%	40%
Pregnancy, %	92	88	73	57
Weaning weight, kg	211	209	197	136
Live weight sold, kg/ha	408	395	332	200

[a] Taken from Nelsen et al. (1982).

[b] The hay was coastal bermudagrass hay of approximately 55% digestibility; the level of feeding was ad lib. or unlimited, 80% of the ad lib. amount, 60% of ad lib. and 40% of ad lib.

An interesting observation was that the herds on lower nutrition required a much larger fraction of heifers as replacements and a larger fraction of the offtake was cull cows as compared to weaned calves.

Another study examined effects of hay quality and management practices in an area of Texas where a lot of hay is grown, but rainy weather usually

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presents a problem during early harvest time. Therefore, producers customarily produce mature, low quality hay. We utilized data from the Texas Agricultural Experiment Station at Angleton to simulate the effects on herd productivity of feeding higher vs lower quality hay and other production practices. One of the options in this area of mild winters is pasture overseeded with ryegrass and fallow cultivated fields seeded to ryegrass. The results in table 3 again emphasize the effect of feeding during the winter on total offtake of a herd.

TABLE 3. SIMULATED HERD OFFTAKE FROM FOUR WINTER FEEDING PRACTICES[a]

Winter feed supplement	Sale weight per cow[b]
Low quality hay, 45% digestibility	176 kg
Low quality hay, + .9 kg cubes[c]	191 kg
Higher quality hay, 55% digestibility	189 kg
Ryegrass[d], pasture	238 kg

[a] Source: Texas Agricultural Experiment Station, Angleton.

[b] Sale weight includes weaned calves and cull cows.

[c] Cubes were 75% digestibility and 20% crude protein.

[d] Ryegrass varied according to stage of growth but always exceeded 65% digestibility and 18% crude protein.

The capability now exists for examining or predicting the effects of different management practices on production systems by use of computer simulation models. These types of models are now being employed with soybeans, cotton, corn and sorghum crops. Beef cattle producers could certainly increase their management efficiency by being able to accurately predict the effect of changing various management practices on an economic as well as production basis. Such a decision support system needs to be available on a current up-to-date basis. A producer asks himself many different questions and often is not comfortable with the basis for his answers. Some questions relate to longer term, advance planning (e.g., the best calving season, crossbreeding system, and breeds to fit production resources, management capability, capital resources and market). Then, there are questions that are unique for each year and season; that is, they are reactive to recent events (e.g., for a dry year, hay is low quality and in short supply; what is expected for next year's calving percentage if different alternatives are followed such as supplement feeding vs no supplement, etc.).

These types of "what if" questions always require experience-based, sound judgment, but the decisions can be aided immensely by examining predicted outcomes and economics on a quantitative basis. The computer hardware and a good deal of the software to do this presently exists, but it is still in the research phase.

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The theme of this symposium is breeding beef cattle. The point was made to breed cattle to match their environment - a variable quantity across time and space. Also, the point was made that there is an optimal level of inputs and that the level of inputs interacts with breedtype. This point is illustrated by the results of a study in a mixed cropping area of Central Texas that examined alternative production practice and market time for that farming area. Data from the Texas Agricultural Experiment Station Research Center at McGregor were used to represent this area (Cartwright et al., 1981). Native summer pasture and winter oat grazing are common. Large, medium and small cattle of high, medium and low milk production (nine types) were included as options. Selling calves at weaning, after stocking or after owning them through custom feeding was examined. A 10-year base of economic data up to 1979 was used to establish price relationships. The results of this study (table 4) indicated that 8 years out of 10, the system that would have had the greatest net return was large cattle with low milk production and calves going directly into custom feedlots after weaning. That is, this strategy resulted in the greatest net returns for this area for the time examined. If either the time or the area is changed then the results may be different.

Summary

I do not think it will be many years before we have available decision support systems (based on systems analysis techniques) to help make long-term and short-term breeding and management decisions for each production area. If this prediction is correct, then we should expect some change in our approach to breeding beef cattle; i.e., we have the tools to allow us to design and manage breeding programs for specific areas, economic resources, etc. in contrast to breeding cattle for general performance characters.

General conclusions from systems analysis studies include the following:

> Increasing or decreasing genetic potential for any of the primary characters (size/age, maturing rate size, and milk production) causes herd production changes that tend to have a counterbalancing effect on net herd productivity efficiency, biological or economic.

> Intermediate values for the primary characters tend to be optimal but vary to different sets of production conditions. As nutritional quality, availability and stability (across seasons and years) increase, the optimal values for the primary characters tend to increase.

> There is an optimal set of primary characters that best synchronizes with each set of production conditions. The characters must also be synchronized with one another to form the optimal set.

> Increasing efficiency of production involves increasing herd offtake (gross revenue), decreasing herd input (costs) or both. Selecting to attain optimal levels for the primary (production) characters tends mainly to increase herd offtake while selection for the secondary (soundness) characters tends to decrease inputs required.

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TABLE 4. SIMULATED PERFORMANCE OF NINE CATTLE HERDS OF THREE DIFFERENT GENETIC SIZES AND THREE DIFFERENT MILK PRODUCTION POTENTIALS FOR A RANCH LOCATED IN CENTRAL TEXAS[a]

Herd performance measures	Genetic potential[b]								
	Large size			Medium size			Small size		
	Heavy milk	Moderate milk	Light milk	Heavy milk	Moderate milk	Light milk	Heavy milk	Moderate milk	Light milk
Avg 8-yr-old cow wt., kg	518	518	519	470	470	471	421	421	422
Avg calving percent	73.0	74.4	76.1	72.6	73.4	74.1	70.2	71.6	72.3
Avg 8-mo wean wt., kg	244	225	212	227	215	202	216	204	191
Avg finished wt., kg[c]	466	480	490	449	454	465	415	428	437
Avg profit per ha, $[d]	4.55	10.85	23.97	2.55	13.57	13.22	-3.29	7.04	17.32

a Adapted from Cartwright et al. (1981). These simulated output figures depend on the prevailing production and market and are presented for illustrating differences in net productivity possible for different practices.

b These sizes may be characterized by mature cows with 25% body fat: large = 545 kg, medium = 500 kg, and small = 455 kg. These milk potentials may be characterized by the production of a well-fed mature cow at peak day location: heavy = 13.6 kg, moderate = 10.9 kg, and light = 8.2 kg.

c Feedlot steers, all finished to same grade: "mostly" (60 to 70%) choice.

d The years examined were 1972 through 1978 but profit figures for the first year only are presented.

In addition, it may be concluded that systems analysis tends to focus more attention on the following:

Specification of selection objectives and criteria to maximize a more clearly defined objective function (e.g., herd profits vs individual animal performance).

The physiological processes (rates and flows) that affect cattle performance.

Integration among disciplines in order to understand biological rates and flows and make final interpretations in economic terms.

The need for basic research (biological processes) in the animal and related sciences.

Systems analysis will not replace the value of experience, good judgment, attention to detail and skilled husbandry, but should incorporate them and become an additional tool that I hope will enhance the personal satisfactions of being a beef cattle producer by enhancing the potential for making a profit with cow-calf operations.

Literature Cited

Baker, J. F. 1982. Evaluation of genotype-environment interactions in beef cattle production systems using a computer simulation model. Ph.D. Dissertation. Texas A&M Univ., College Station.

Cartwright, T. C. 1970. Selection criteria for beef cattle for the future. J. Anim. Sci. 30:706.

Cartwright, T. C., K. W. Stokes, J. W. Stuth, T. C. Nelsen and D. E. Farris. 1981. Evaluation of effect of cow size and milk production on herd productivity in Central Texas. Texas Agr. Exp. Sta. CPR 37.

Cartwright, T. C. 1982. Objectives in beef cattle improvement. Proc., World Congress on Sheep and Beef Cattle Breeding. Vol. II, p. 19. Denmore Press, Palmerston North, N.Z.

Doren, P. E., C. R. Shumway, M. M. Kothmann and T. C. Cartwright. 1984. An economic evaluation of simulated biological production of beef cattle. J. Anim. Sci. (Prepared for submission).

Forrester, J. W. 1968. Principles of Systems (2nd Ed.) MIT Press, Cambridge, MA.

Johnson, D. E. 1984. Impact of maintenance on cow efficiency. Proc., Beef Cow Efficiency Forum, Michigan State Univ. and Colorado State Univ.

Nelsen, T. C., T. C. Cartwright, A. K. Angirasa and F. M. Rouquette, Jr. 1982. Simulated effects of calving season and winter hay feeding level on cow herd productivity. J. Anim. Sci. 54:29.

Sanders, J. O. and T. C. Cartwright. 1979a. A general cattle production systems model. I. Structure of the model. Agr. Sys. 4:217.

Sanders, J. O. and T. C. Cartwright. 1979b. A general cattle production system model. II. Procedures used for simulating animal performance. Agr. Sys. 4:289.

Spedding, C. R. W. 1979. An Introduction to Agricultural Systems. Advanced Science Publishers, London, p. 169.

APPLICATIONS OF NEW TECHNOLOGY

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It might seem that the most difficult job on this program would be to pre-
dict applications of new technology to range cattle breeding. After all,
molecular biology, biotechnology and computer science all are changing
rapidly. Those of us with a major interest in the application of science to
livestock agriculture barely have time to grasp one advance before another
is announced. Things that seem feasible today, we wouldn't have dreamed of
at a symposium honoring the 10th, 25th or even 40th birthday of Line 1. In
the words of science fiction author, Arthur C Clarke, "The future isn't what
it used to be".

My task isn't as difficult, though, as it might be because I have access to
a crystal ball. Granted, it is subject to brownouts, and its solid-state
circuits sometimes go haywire. Nevertheless, it allows me to look at the
Fort Keogh Livestock and Range Research Laboratory in 2009, where a sym-
posium is in progress commemorating the 75th anniversary of the founding of
Line 1.

You would hardly know the place. That very high rise building toward the
river houses the Administration Section. In the 1990's, there was a major
increase in funding for range cattle research. As the science expanded,
administration expanded with it. The USDA adopted a formula requiring one
administrator per .80 scientist, .25 technician and .20 farm or ranch
worker. Unfortunately, the formula also required one new administrator per
.15 old administrator. Brad Knapp has been working on the problem ever
since, trying to approximate a limit to the infinite administrative
progression that the new rule generated.

Over there, where silage used to be grown, is the molecular biology complex.
The isolation of genes and DNA segments using restriction enzymes, DNA
sequencing and synthesis and gene transfer between and within species, along
with other advances, caused an embarrassing situation for cattle breeders
back in the 1980's. We didn't know of many genes worthy of isolation and
transfer. Some of us had even forgotten (or hadn't learned in the first
place) our classical genetics. We had to relearn that Mendel was not a
Billings used car dealer and that meiosis was not a sexually transmitted
disease of cattle. But we coped. Retrenchment was followed by years of
basic research into the biochemistry and physiology of growth, reproduc-
tion, senescence, behavior and health. Gradually we learned of genes truly
worthy of transfer, and the beef cattle molecular biologists have been gain-
fully employed ever since.

A large section in molecular biology is devoted to tissue culture or, more
specifically, to in vitro performance testing of all lines from embryos,
zygotes and intact animals. Enzymes, antigens, receptors, reaction rates
and biochemical traits important to range cattle performance are being
assayed in the cells.

Before this research became feasible, major efforts were exerted to screen range populations for truly outstanding individuals. Cows were identified that produced healthy calves with regularity and that efficiently produced milk at a level allowing reasonable expression of offspring growth potential. Bulls were identified with optimal growth rates, exceptional digestive and biosynthetic efficiency, and excellent carcass composition and quality. Other bulls were identified with exceptional libido, fertility, semen quality and quantity - and the ability, while blindfolded and ear-plugged, to detect a heifer in estrus from 200 meters upwind. Cattle of both sexes were identified with exceptional health in the face of exceptional microbiological, parasitic and environmental challenge. In several cases, resistance to viral diseases was associated with loci in the major histocompatability complex coding for particular lymphocyte surface antigens. In other cases, alleles were identified that caused more rapid proliferation of lymphocytes upon challenge by a foreign antigen. Those with high tolerance to toxic plants, nutritional deficiencies and nutritional excesses also were found. Individuals were identified with behavior patterns especially desirable to the cattle raiser. Good selective grazers were found, as were good mothers and individuals with the right combination of tractability and wariness.

Before molecular biology, unusually outstanding individuals such as these were oddities - subject to admiration and wonder - but opportunities to "harvest" their genes (in combinations likely to be exceptionally beneficial to their descendents) were minimal.

Cell lines were developed from these individuals and from their mediocre and inferior contemporaries. Basic chemistry was then performed on the cell lines to screen for genetic and biochemical reasons separating the "sheep from the goats" and the "wheat from the chaff" (to mix agricultural metaphors). Many important biochemical traits were identified. Not many geneticists were surprised to find that a genotype conferring excellence for one important trait often was associated with poor performance for others. We had begun to expect in the 1980's that pleiotropy was common - perhaps Mother Nature's main weapon to thwart our efforts to select the perfect beast. We were, however, surprised at the frequency with which gene combinations (the epistasis we always swept into the error term) were associated with exceptional performance. This made beef cattle gene engineering more difficult but also more interesting. The search for biochemical excellence goes on.

Another wing of the molecular biology complex is devoted to extrachromasomal inheritance. Mitochondria have come into their own, and researchers are actively testing mitochondrial complementation. They have created cells with graded proportions of mitochondria from Bos taurus, Bos indicus and other Bos species. Mitochondria isolated from feral cattle populations, subjected for many generations to natural but no artificial selection, are also tested in traditional beef cattle cell lines and in intact animals. So far, it appears that cattle mitochondria have not suffered from the relaxation (or altered emphasis) of natural selection brought about by husbandry, but not all of the results are in. Also, gene transfers from mitochondria of other species to cattle mitochondria have been accomplished. In vivo evaluations

of the results are still in progress. The extrachromosomal inheritance group is also involved in identifying viral and other vectors potentially useful as DNA transfer agents.

That small building out back houses the new laboratory animal colony. Notice the concrete and steel construction. Plans originally called for wood, but the folly of that suggestion was discovered just in time. You see, the new model organism is the termite. Legislators asked to fund the colony were unimpressed until it was pointed out to them that termite gastrointestinal micro-organisms fulfill a role in that symbiotic relationship similar to rumen microflora in cattle. In the colony, biochemists are working on digestive physiology, and modellers are studying dynamics of the relationship between microflora and host. Experiments have been conducted to transfer genes from termite micro-organisms, and even from marine wood-eating worms, to rumen microbes. The scientists are trying to create cattle capable of utilizing wood wastes. Oregonians are watching this research with great interest, but results are not yet in.

Across the old parade ground is the Biotechnology building, the ground floor of which is devoted to in vitro inbred line formation. After Line 1 was toasted by beef cattle geneticists back in 1984, scientists decided to use biotechnology to accelerate F within the line. Embryos were collected, and one pronucleus from each was removed by microsurgery. Chromosomes of the remaining pronucleus were allowed to replicate but cell division was prevented chemically. Embryos were then allowed to develop according to the regular laws of mitosis. Resultant calves were completely homozygous; their inbreeding coefficient became 1.0 in one generation. They also should all have been female; because any embryo whose remaining pronucleus carried a Y chromosome became, upon chromosome replication, YY and died. To circumvent this difficulty, the scientists called upon their colleagues specializing in embryo splitting and cytogenetic micro-surgery. Inbred female embryos were split, then one of the X chromosomes from each cell of one-half embryo was removed and replaced with a donor Y. This brought about the logical inconsistency of identical twins of unlike sex, and it allowed perpetuation of the inbred sublines by sexual reproduction.

It did not surprise the embryo surgeons that the success rate for inbred subline formation was very low. They expected to lose all the YY zygotes plus all embryos in which a lethal gene became homozygous. The small proportion of successes were, though, free of lethals; and many genotypes were created for biochemical, physiological, behavioral and performance testing. Since each success essentially represented a unique meiotic experiment, Line 1 now has numerous sublines, beginning with 1:1 and now up to 1:143. As in cattle inbred line development starting back in the 1940's, many of the lines have little to offer, but some few others have great promise for future commercial exploitation. And, the sublines could be crossed to recreate Line 1--absent of lethal genes (plus others lost from "drift" in the meiotic shuffle).

Not here at Fort Keogh but at other locations, the techniques of cytogenic micro-manipulation are being used for a variety of purposes. Both in cell lines (in tissue culture) and in cultured embryos, individual chromosomes

or chromosome pairs are added or removed to create nullisomics, monosomics, trisomics and higher multiples at will. This work has been useful to map genes and to determine biological effects of extra or missing enzymes. Removed chromosomes are sometimes replaced by homologous donor chromosomes from another individual from the same breed, from a different breed or even from a different species. Among other things, epistasis is being examined. That is, what is the effect of a particular chromosome pair in an alien genetic background?

Somewhat more futuristic are attempts to synthesize, from chromosome pools, individual cells with chromosomes from a variety of donors. Some very unusual and interesting breed and species crosses may result from this work.

The second floor of "Biotechnology" houses the cloning unit. This technology still isn't routine, but it has progressed a long ways from the old embryo splitting days. It is now possible to transplant nuclei from adult donor cells into enucleated ova and very early embryos. Although it is costly, clones of up to a couple of dozen contemporary individuals can be produced.

This has, of course, been a boon to quantitative genetics researchers. For one thing, they have found the clones extremely useful for genetic x environment interaction studies. Their experiments have established that genetic x micro-environmental interactions can be important. Cattle really do vary in their relative adaptation to physical and management environments within an ecological zone. It is not yet possible, though, to predict ahead of time what genotypes will fit what micro-environments. Cattle cannot yet be synthesized to fit a specific environmental niche.

Clones also have been used in combination with other types of relatives to partition environmental, additive and nonadditive genetic variation. It has been established from these experiments that nonadditive gene effects are important for certain traits - behavior and parasite resistance, for example. Thus, gene engineering to create desirable genotypes for such traits will have to involve constellations of rather than single loci.

Also, on the second floor, is the section devoted to research and applications in sex selection. At this point, the crystal ball gets rather foggy, but it looks like several approaches are close to success. Even back in 1984, researchers could separate X- from Y-chromosome-bearing sperm cells (and count them) by flow cytometry, but required stains were fatal to the cells. It appears that separation can now be achieved without killing the cells. Other scientists are working on immunizations to favor one or the other sex of offspring. Reproductive immunology (or immunological reproduction) is an active field. Others are working in semen separation with a variety of physical and biochemical treatments. Modellers and geneteconomists are devising programs to use sex selection maximally to increase range cattle production efficiency.

The third floor of the Biotechnology Building houses the scientists working on embryo fusion - or induced chimerism. This is one biotechnology for which there is considerable commercial application. As artifical insemination companies became successful in the 1950's and embryo transfer companies

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grew in the 1980's, chimera companies are now expanding. Embryos are fused to create individuals of the most appropriate type for broad environmental, management and economic needs. Here in Montana, for example, a hexaparental calf with Hereford, Angus, Charolais, Tarentaise, Brahman and Bison parentage is popular. In the Gulf Coast states, Brahman, Angus, Gelbvieh, Red Sindhi tetraparental calves are popular. Another company is marketing straightbred induced chimeras that have four or six different alleles at specific disease-resistant loci, a counterpart of the old broad-spectrum antibiotics.

Although embryo fusion is a mature technology being used commercially, induced chimerism is still an active research area. The LARRL scientists are developing methods to create chimeras with predictable graded proportions of inheritance from the various donor parents. Rather farther down the road are attempts to create chimeras in which different tissues and organs trace to different desired ancestries. For example, they might try to create a calf with the musculature of a Limousin and the hide and gastro-intestinal tract of a Brahman. How they expect to accomplish this is a closely guarded secret, even to my crystal ball.

The top floor of Biotechnology is devoted to immunology. One group of technical personnel provides monoclonal antibody support to scientists throughout the Station. Projects of the research immunologists include efforts to control offspring sex, to trigger puberty, to synchronize estrus and to enhance growth rate by immunization to an individual's own hormones.

Major efforts are underway to enhance genetic resistance to disease. Some interesting relationships have been discovered between passive and active immune mechanisms and between cellular, humoral, and complement aspects of the active immune system. For many immunological traits, the scientists have concluded that stabilizing as opposed to directional selection is in order. Pleiotropy strikes again. As one example, selection for increased antibody response to a certain antigen also caused increased nonspecific antibody response to unrelated antigens, due to increased multiplication and differentiation of antibody-producing lymphocytes. In those same animals, though, macrophages were less efficient at catabolism of the ingested antigen (although no change in the rate of phagocytosis or engulfment of the antigen was seen). The antigen was present, in an unaltered condition, for a longer time and, therefore, stimulated a greater response. In this case, cellular immunity was not affected by the change in humoral response.

The old headquarters and laboratory building has been taken over by the computer center, the modeling group, the planned mating service center and the statistics support group.

Dramatic improvements in computer speed and memory and in programming skill that were evident in the 1980's have continued but may now be tapering off. It is now possible to solve, quickly and economically, enormous numbers of mixed model equations. Breeding value estimation from BLUP-type methods (my crystal ball can't make out the acronyms that superceded BLUP, REML and MINQUE) is now a finely-tuned science and a routine procedure. We can now compute EBV and its accuracy for single traits or for aggregate genetic

value from any combination of traits on an individual and on any combination of its relatives. Nonlinear economic values, situations in which the economic value of one trait is dependent upon phenotypic merit for another and situations in which economic values vary with physical and management environment are built into the programs, as are allowances for restricted or stabilizing selection on some or all traits.

In addition to studies already cited in cooperation with molecular biologists and biotechnologists, the modelling group is doing some very interesting work. One experiment involves the concept from evolutionary genetics of group selection. The modelers are determining whether beef cattle populations synthesized from specific combinations of individuals of different genotypes would be more "fit" than naturally or randomly associated herds. (They have redefined "fitness" as bioeconomic efficiency as opposed to Darwinian or reproductive fitness.) Implicit in their model is the concept that the merit of a particular genotype might be dependent upon genotypes already present in the herd. In a sense, they are testing the importance of genetic x genetic x environmental interactions. That is, within and across environments, do genotypes within a herd interact? They have had to enlist support from animal ecologists and ethologists, as well as of range scientists, biometeorologists and economists. If their theories are correct, then it will be beneficial to synthesize herds for specific environments, as well (perhaps) as individuals for specific needs.

As stated earlier, there also is a considerable modeling effort devoted to computing the asymtotic number of LARRL administrators.

Since the mating season for fall calving is just around the corner, things are busy at the planned mating service center. Australian work in poultry and German work in cattle in the 1970's and 1980's established that heterozygosity at biochemically identifiable loci could be associated with traits of reproductive fitness. In chickens, the affected trait was egg production per unit of time; and in cattle, the trait responding favorably to increased proportion of heterozygous loci was fertility. This work was confirmed in later investigations, and several segregating loci were identified in which overall bioeconomic efficiency was influenced in an overdominant fashion. Other loci acted additively and others in a dominant vs recessive manner and many, of course, had no measurable association with efficiency at all.

How, you might ask, might a planned mating service use this information? Genotypes for the important loci are determined for all available service sires and the data are banked at the center. Cows likewise are typed for the relevant loci. Each cow is then test mated, by computer, to each available service sire. The distribution of phenotypic merit of possible calves from each mating is simulated, and the mean and variance of the distribution is computed. The most appropriate mating is then chosen based upon the mean (or expected value) of a calf and the variance (uncertainty or risk) of the distribution. Choice criteria in the program can readily be altered according to the type of enterprise (seedstock vs commercial) and the intended use (replacement vs market animal) and sex of the calf. The planned mating concept might also be used to aid in the selection of

range bulls. An entire cow herd could be typed for the relevant loci, along with the group of bulls considered acceptable according to other criteria. Each bull could then be "test mated" by computer to the entire herd, and the distribution of possible calves simulated. As above, the mean and variance of the distribution from each bull could be compared to rank the bulls and possibly to establish different monetary values for each of them.

This may seem pretty far-fetched but, remember, how far computer and biochemical technology have come since 1984.

Even in statistical support, times have changed. Analysis of variance and covariance and multiple regression analyses are still in general use. Statisticians agree that they are perfectly appropriate for many situations. Scientists have stopped using them so indiscriminantly for all-or-more traits, however, relying more often on other methods, including discriminate analysis. Multivariate techniques have become much more widespread as more and more people understand the meaning of eigenvalues and principal components. It has become much less common to find linear methods applied to situations in which curvi-linear relationships are likely to be encountered. Response surface methodology has found many applications in genetics and in nutrition, physiology and economics as well.

Theoreticians finally have provided us with computation formulas for standard errors of genetic parameters that are not estimations. Lo and behold, these true standard errors are even larger than our oldtime approximations. Some help has come from the concept inherent in the use of Bayes Theorem, as popularized by Illinois workers back in 1984 (and as I understood it at the time); the concept is that previously collected information should be utilized, along with data collected from a current experiment, in conducting tests of hypothesis and establishing probabilities for type I error. The concept has been expanded to allow information in previous genetic parameter estimates to contribute to (and reduce the standard errors of) current estimates. Thus, genetic parameter estimates, with usefully narrow confidence ranges, now exist for and among all of the "old" and many of the "new" traits important to range cattle production efficiency.

Finally, statistical support personnel are more alert (than was formerly the case) to possible applications in agricultural science of statistical procedures in use by their counterparts in the physical and social sciences.

That concludes our tour of Fort Keogh in 2009. It's a good thing, as my crystal ball has just suffered a terminal short. I am sure you will realize that this whimsical look into the future is nearly certain ($P<.0001$) not all to come to pass. Indeed, perhaps all of it is unrealistic. Not being a practitioner of molecular biology or biotechnology or computer wizardry or theoretical statistics, I am much more free to speculate than one who really knows about that of which he speaks. I hope, though, that I have argued convincingly that "the sky's the limit" and that new technologies are very likely to make an important impact upon the range beef cattle breeding business.

In the words of Mort Sahl, "The future lies ahead". I'm looking forward to seeing you there.

Literature Cited

Barker, J. S. F., K. Hammond and A. E. McClintock. 1982. Future Developments in the Genetic Improvement of Animals. Academic Press, New York.

Brackett, B. G., G. E. Seidel, Jr. and S. M. Seidel, Editors. 1981. New Technologies in Animal Breeding. Academic Press, New York.

Dickerson, G. E. and R. L. Willham. 1983. Quantitative genetic engineering of more efficient animal production. J. Anim. Sci. 57(Suppl. 1):248.

Hierl, H. F. 1976. Relationship between heterozygosity as estimated from genetic marker and fertility in cattle. Theor. Appl. Genet. 47:77.

Mouton, D., C. Stiffel and G. Biozzi. 1981. Genetic regulation of high and low immunoresponsiveness. In: M. E. Gershwin and B. Merchant (Ed.) Immunologic Defects in Laboratory Animals. Vol. 1:19-47, Plenum Publ. Comm., New York.

Rutledge, J. J. and G. E. Seidel, Jr. 1983. Genetic engineering and animal production. J. Anim. Sci. 57(Suppl. 1):265.

Sheldon, B. L. 1980. Perspectives for poultry genetics in the age of molecular biology. World's Poultry Sci. J. 36:143.

Effect of forage quality on 24-hour rumen fermentation, liquid flow patterns and organic matter intake in beef steers grazing native range. R. C. Cochran* and D. C. Adams. Ft. Keogh Livestock and Range Research Station, USDA-ARS and Montana Agr. Exp. Sta., Miles City, MT 59301

Eight rumen (RF) and 5 esophageally fistulated beef steers grazed a broken upland range site from May 4 to November 5, 1981 in a study to characterize changes in 24-h rumen fermentation, liquid passage and organic matter intake (OMI). Six 8 d trials were conducted in one 52 ha pasture. Trials began on May 7, May 22, June 19, July 30, September 11 and October 28, 1981. On d 1 of each collection period RF steers were dosed with CoEDTA. Rumen samples were collected at 0700 (before dosing), 1100, 1500, 1900, 2300 and 0300 h and analyzed for pH and concentrations of volatile fatty acids (VFA), NH3 and Cobalt. During d 2-8 RF steers were fit with fecal bags for total fecal collections. Esophageally collected range forage was analyzed for crude protein, acid detergent fiber (ADF), acid detergent lignin, organic matter and in-vitro organic matter digestibility (IVOMD). Crude protein content of the range forage decreased with advancing maturity (14.3 to 7.0%) whereas ADF increased from 38.1 to 47.7%. The IVOMD with advancing season were 71.6, 72.1, 74.2, 66.9, 62.6 and 63.8%, respectively. Total VFA and NH3 concentrations, molar proportions of VFA and pH varied over a 24-h period. However, changes in these variables were dependent (P<.01) upon date. The 24 h profiles for principal VFA, acetate to propionate ratio (A:P ratio), branched chain VFA (BCVFA), and NH3 displayed grouping associated with forage maturity. Profiles from May and mid-June (early profiles) clustered together and late profiles (late July to early August, mid-September and late October) displayed grouping. Early profiles for propionate, butyrate, BCVFA and NH3 were associated with higher molar proportions and concentration, respectively, when compared to late profiles. In contrast, lower molar proportion of acetate and lower A:P ratio were observed in early profiles compared to late profiles. Profiles for BCVFA displayed greater variation across 24-h periods than did profiles for major VFA and A:P ratio. Early NH3 profiles displayed larger diurnal variation than late NH3 profiles. Grouping was not as evident in 24-h profiles of total VFA concentration, molar proportion of valerate and pH. Total VFA and valerate profiles displayed considerable variation over a 24-h period, however, early profiles were associated with higher concentration and molar proportion respectively. Profiles for pH were tightly clustered. Some values in the September and October profiles were lower than expected (5.6 - 5.8). Liquid passage characteristics were affected (P<.01) by forage maturity. Rumen liquid volume increased with advancing forage maturity (22.8 to 83.3 1) but dropped slightly in October (65.0 1). Liquid dilution rate (LDR) decreased up to September (18.3 - 8.8%/h) but increased slightly in late October (10.1%/h). Autumn precipitation was observed. Organic matter intake also varied across dates (P<.01). Early May and Late July intakes were slightly higher than other periods (2.1 and 2.0% of body weight, respectively). We conclude that advancing forage maturity was associated with decrease in VFA (molar proportion of acetate increased), NH3, pH and LDR, however, changes were not linear. Changes in OMI over the range of forage maturities studied were small.

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SLAM Simulation of Energetics of Cow-Calf Production. C. A. Dinkel, Department of Animal and Range Sciences, South Dakota State University, Brookings, South Dakota, 57007.

One hundred forty-one records from 61 two-year-old Simmental x Hereford rotation cross females and 80 straight-bred Hereford and Angus x Hereford rotation two-year-old females and their calves produced in 1978, 1980, 1981, 1982 and 1983 were used to derive cow and calf energy partitions for each of the groups for the mid-gestation (P1), last trimester (P2) and lactation (P3) periods of the cow year. The fixed model (SAS, GLM) included the discrete effects of year and the covariates for maintenance weight (MWT), weight change (CWTC), days in the period in P1 and P3 and milk production in P3. The dependent variable was the measured TDN intake (kg) for each period for each cow.

	Intercept	MWT	CWTC	MILK
Mid-gestation (P1)				
AxH & H	123.829	.639	.581	
SxH	128.059	.527	.633	
Last Trimester (P2)				
AxH & H	187.177	.649	.367	
SxH	241.463	.540	.298	
Lactation (P3)				
AxH & H	682.601	1.537	.2990	13.730
SxH	703.746	1.725	.2820	11.359

The energy partitions were used in the SLAM model which requires as input cow size, milk production, birth weight, weaning weight, cow weight change P1, cow weight change P2 and cow weight change P3. The program calculates and provides in either tabular or plotted form: (1) calf energy requirement from the range, (2) cow weight, (3) calf weight, (4) cow energy requirements from the range, (5) milk production and (6) total cow plus calf energy requirements. Choice of time interval (e.g., daily) is available. The British breed energetics have been validated utilizing individual feeding data for Hereford cows provided by the University of Wisconsin. Prediction of cow energy requirements were within 9% and calf requirements 16% of measured consumption. Differences in methods of measuring milk may influence the latter. Predictions using an earlier energy partition of data from mature Angus, Charolais and reciprocal cross cows were within 6% of measured consumption. Validation of the Simmental x Hereford partition is still pending.

Energy Partition, Simulation, Beef Cattle

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Effect of Breed and Mating System on Weaning Production in Beef Cattle. M.D. Monfore, C.A. Dinkel and W.R. Trevillyan. South Dakota State University, Brookings.

Thirteen hundred seventy-nine records from 396 straightbred Hereford (HH), 421 Angus-Hereford (AH) and 562 Simmental-Hereford (SH) cows and their calves produced from 1974 through 1983 were utilized in a fixed model analysis (Harvey's Least Squares) to evaluate effect of breed and mating systems on weaning production. Thirteen models were used which included effects of breed of dam (BOD), sex of calf (SEX), year (YR), age of calf (AOC) and age of dam-management nested within year (AMYR) in appropriate combinations with dependent variables calving percent of cows exposed (CALV%), weaning percent of cows exposed (WEAN%), calf weaning weight (WWT), gestation length (GEST), percent first service conception of cows calving (CONCEP), Julian calving date (DOB), calf birth weight (BWT), cow weight at weaning (FLWT) and cow weight change during lactation (WTCHNG). Each model was run twice with BOD coded as the three major breed classes (RUN1) and with BOD coded in 7 classes based on the percentage of Hereford in each breed combination (RUN2). AH and SH dams were bred according to a two breed rotation scheme while HH dams were maintained in a purebred system. All animals were maintained under western South Dakota range conditions at the Antelope Range Livestock Station. Least squares means for each breed group were as follows:

---RUN1---

BOD	NO.	CALV%	WEAN%	WWT*	GEST*	CONCEP	DOB	BWT*	FLWT*	WTCHNG*
HH	369	85.9	80.0	197.8	285	.86	91	35.4	474.9	+61.7
AH	421	89.1	85.7	213.5	285	.82	90	35.4	445.4	+52.2
SH	592	90.7	83.1	230.8	287	.80	92	29.9	517.6	+57.2

---RUN2---

BOD	(%HH)	NO.	CALV%	WEAN%	WWT*	GEST*	CONCEP	DOB*	BWT*	FLWT*	WTCHNG*
HH	(100)	396	86.0	80.1	198.2	285	.88	92	35.4	471.5	+57.9
AH	(75)	46	86.2	81.9	212.3	284	.72	88	36.3	491.2	+51.7
AH	(50)	325	89.8	86.4	213.2	285	.84	92	35.4	439.5	+48.4
AH	(25)	50	90.4	84.5	214.1	284	.84	84	34.9	420.5	+69.5
SH	(75)	158	93.8	84.4	227.7	287	.78	91	41.3	520.3	+70.7
SH	(50)	379	89.6	82.7	232.7	286	.82	93	39.0	513.5	+61.6
SH	(38)	25	87.7	81.1	234.0	290	.67	96	39.9	527.5	+48.7

* P<.05

No breed group differences were found (P>.05) in RUN1 for CALV%, WEAN%, CONCEP or DOB. No Breed differences were found (P>.05) in RUN2 for CALV%, WEAN% or CONCEP. These results indicate similar reproductive efficiency among breed groups. Important breed differences were found (P<.05) for WWT, BWT, FLWT and WTCHNG. Within systems, higher levels of Simmental breeding yielded lower WTCHNG and higher WWT, DOB, BWT, GEST and FLWT values than other breed groups. Higher levels of Angus breeding resulted in lower BWT, FLWT and DOB.

Key words: Cow Breeds, Mating Systems, Weaning Production.